Benthic assemblage development and larval ecology of marine invertebrates at Adelaide Island, Antarctica

Thesis

Benthic assemblage development and larval ecology of marine invertebrates at Adelaide Island, Antarctica

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by

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Abstract

This thesis describes the first regularly resurveyed study of marine benthic colonisation processes at a location within the Antarctic Circle (66° 30′ S). Invertebrate assemblages on hard substrata were studied at 8 m and 20 m depths at three locations near Rothera Point, Adelaide Island (67° 34′ S, 68° 07′ W). Assemblages on natural substrata were surveyed photographically and by sampling of cryptic sessile fauna. Recruitment to upper and lower surfaces of artificial substrata was monitored at monthly intervals through 1.5 yr and subsequent survival and growth of sessile assemblages was monitored photographically over 3 yr. Planktonic larvae of benthic invertebrates were surveyed at monthly intervals through 1.5 yr.

Recruitment took place throughout the year but was strongly seasonal in most taxa. Many sessile taxa recruited during winter; apparently in direct contrast to a general pattern of summer recruitment in temperate latitudes. All vagile taxa, by contrast, recruited in summer, regardless of developmental type or time of spawning. Rates of assemblage development, and maximum growth rates of individual species, were slow compared with temperate latitudes but abiotic and biotic disturbances caused realised growth rates to be highly variable at scales of m – km. Ice impacts affected substrata at 8 m but the establishment of assemblages at both depths was controlled principally by post-settlement mortality from biotic disturbances, particularly grazing by the urchin *Sterechinus neumayeri*.

Larvae were present in all months but most taxa showed strong seasonality of occurrence. Diversity of larval types was comparable with data from other Antarctic and temperate studies but abundances were higher than in a similar study at Signy Island (60° 43′ S, 45° 36′ W). The range of larval types, durations, and times of spawning argues against any strong selective pressures acting on developmental mode itself. Rather, the timing of settlement appears to be the characteristic of the life cycle that is most strongly selected for. It is suggested that differences between sessile and mobile taxa in the timing of settlement may be caused by the seasonal availability of food types for juvenile stages.

Acknowledgements

I had no intention of going to the Antarctic: bare-foot in the tropics was my preferred mode and marooning myself in the ice for the better part of three years held little appeal. Within half an hour of meeting Andy Clarke and Lloyd Peck in the interview for this project, however, I was convinced that this was going to be the best job in the world. Having had some time to consider things now, I think I was not far wrong in my initial assessment.

Andy and Lloyd initiated the study as part of their ongoing research progamme at the British Antarctic Survey and their enthusiasm and intellectual curiosity were largely responsible for changing my mind about cold places. As if more enthusiasm were needed, Dave Barnes became my line manager part-way through the project and with the combined intellects and experience of these three for guidance, I was fortunate indeed: many thanks to all three for help, advice, and support throughout.

The success of the study was completely dependent on the support of the team at Rothera. Many people helped over the two years and without the support of the entire BAS organisation a project such as this would have been impossible. In particular, without the hard work, good-humour, adaptability, and friendship of Phill Horne, Rayner Piper, Will Gilchrist, John Burleigh, and Mairi Nicholson the project would have been a lot less enjoyable, a lot harder, and a lot less successful than it was. Thanks especially to Phill and Rayner for sticking with it when the Bonner Laboratory burned down, and to everyone who helped to get us back in the water again: I'm still amazed that we achieved what we did. Thanks too to Paul Rose for relentless optimism at the start of the project and some memorable dives setting up the recruitment study.

Back in the UK, Doug Bone built a new plankton net, Andrew Fleming and Paul Cooper helped with image analysis problems, Peter Fretwell created maps, Peter Rothery advised on statistical analyses, Katrin Linse helped with identifications and ideas, Pete Lens and Andy Wood sorted IT problems, and Christine Phillips sought out obscure references. Chris Todd made valuable suggestions during the analysis period, and correspondence with Paul Dayton made me think a lot.

Finally, many thanks to friends and family who stayed in touch while I was away and especially to Kate for everything.

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INTRODUCTION

This project investigates the colonisation of hard substrata in the Antarctic shallow sublittoral. Nearshore benthic ecosystems have been studied extensively at lower latitudes (e.g. Coe & Allen 1937, Thorson 1946, Osman 1977, Ayling 1981, Todd 1998, Hughes et al. 2002) but there have been few successful studies in this area of research in polar seas (Dayton 1990, Arntz et al. 1994). Consequently, the processes controlling the establishment, maintenance, and growth of assemblages in these habitats remain poorly understood. If general principles governing benthic ecosystems are to be defined it is important that there should be reliable data from a broad range of environments and particularly from the most extreme, not just the most accessible.

The Antarctic nearshore environment is of immediate interest because of the unique combination of extremely low but relatively constant seawater temperatures, highly seasonal primary production which is effectively decoupled from temperature effects, and routine disturbance of the sea-bed by ice. Furthermore, the biogeographic isolation and relative constancy of environmental conditions in Antarctica through evolutionary time also afford the potential for assessing the generality of some broader ecological concepts. In particular, the relative importance of selective pressures acting on different phases of the life cycle might be best assessed in an environment in which the critical variables of temperature and seasonality of production are at their most extreme values.

The study divides into four main sections which investigate different aspects of benthic assemblage development and thus different life history stages:

1) a survey of benthic assemblages on natural substrata,

2) a study of short-term recruitment to artificial substrata,

3) a longer-term study of survivorship and growth following initial recruitment,

4) a survey of planktonic larvae of benthic invertebrates.

The first section is a quantitative description of the benthos in the study area and provides the context within which the processes investigated in subsequent sections take place. The second and third sections examine the short-term seasonality of recruitment

through a full year and the development of assemblages over three years. These sections, therefore, deal with the timing and abundance of settlement and assess subsequent survivorship and growth. The fourth section attempts to link larval strategy with adult mode, the timing and success of recruitment, and the seasonality of the environment.

The present chapter introduces the broader ecological and physical contexts in which the study was conducted. This includes an overview of shallow water benthos in the context of global oceanic productivity, a description of fundamental differences in life histories within the benthos, a discussion of the significance of larval reproduction, and a section outlining the environmental characteristics and geological history of Antarctic coastal seas. The chapter concludes with a summary of previous research in this area and a statement of the specific aims of the present study.

MARINE BENTHOS

Context

The oceans cover more than 75% of the Earth's surface and support approximately half of total global primary production (Longhurst et al. 1995, Liu et al. 2000). The most productive regions, however, are the shallow coastal seas and associated continental shelf areas. These represent only ~8% of total ocean area but contribute ~20% of global ocean primary production (Liu et al. 2000). In shelf areas, replenishment of nutrients by wind- or tidally-induced upwelling, and the availability of light for photosynthesis, promote high levels of primary productivity (Longhurst 1991, Sakshaug et al. 2000). In oceanic waters the extended sinking time of biological particles allows a greater proportion of this material to be recycled in the water column through heterotrophic consumption and microbial degradation. In shallow coastal and shelf waters, however, a significant proportion of total water-column primary production sediments directly to the seabed (Gooday et al. 1990, Honjo 1990, Bienfang & Ziemann 1992, Liu et al. 2000). This food source has enabled the proliferation of the diverse and abundant benthic faunal assemblages characteristic of continental shelf areas at all latitudes.

As continental shelves constitute one of the largest habitat types on Earth, secondary production by benthic fauna may also play a significant role, globally, in the sequestration of carbon from the atmosphere. Little work has been done on potential effects of changing climate patterns on benthic secondary production but many of the

predicted changes in climate are associated with sea-level change and thus will directly affect shelf areas. Modification of upwelling systems through changes in atmospheric circulation, and the exposure of previously ice-covered areas of shallow polar seas through the disintegration of ice-shelves are possible consequences and would have immediate impacts on both planktonic and benthic production.

Marine benthic assemblages on hard substrata are characterised by similar organisms worldwide. Calcareous polychaetes, sponges, ascidians, bryozoans, corals, and hydrozoans are common components of sessile assemblages from the tropics to the poles (e.g. Meadows 1969, Osman 1977, Jackson & Winston 1982, Todd & Turner 1986, Tyler & Zibrowius 1992, Holmes et al. 1997, Stanwell-Smith & Barnes 1997, Smith & Witman 1999, Lin & Shao 2002, Barnes & Kuklinski 2005) and it is not uncommon for genera to be globally distributed (e.g. *Spirorbis*, *Celleporella*, *Ascidia*, *Alcyonium*). Similarly, echinoderms, errant polychaetes, molluscs, and a wide range of other mobile taxa are present in benthic assemblages at all latitudes and depths. Such assemblages, therefore, potentially allow comparisons of the effects of environmental variation on basic biological and ecological processes to be made between regions. The relative ease with which such assemblages can be studied and manipulated, and their suitability for investigation by means of non-destructive photographic techniques and artificial substrata further enhance the potential for regional or latitudinal comparisons (e.g. Schoener et al. 1978, Holmes et al. 1997, Witman et al. 2004).

Life histories

Benthic invertebrate assemblages exhibit extraordinarily high taxonomic and trophic diversity but organisms can be classified initially into two broad groups based on adult mode: sessile and mobile. Adults of sessile organisms live attached to the substratum and thus are unable to change their location other than by dislodgment, fragmentation, or rafting. Mobile organisms are able to move across the seabed to seek out food, habitats, mates or other resources. This distinction is associated with differences in feeding mode. Sessile organisms consume food particles suspended in the water column (seston). Depending largely on the physical size of the feeding apparatus in different taxa, these particles may include phytoplankton cells, resuspended organic detritus, or zooplankton, including the planktonic larvae of benthic organisms. Mobile organisms, by contrast, exhibit a wide variety of trophic modes including suspension feeding (e.g. crinoids,

holothurians), deposit feeding (e.g. terebellid polychaetes, holothurians), grazing (e.g. gastropod molluscs, echinoids), and predation (e.g. errant polychaetes, nemerteans, gastropod molluscs). As the techniques used in the present study do not record faster-moving mobile taxa, such as errant polychaetes and amphipods, the term *vagile* is used here to denote taxa which are sedentary but capable of directed movement when adult.

A second fundamental distinction can be made between unitary organisms and modular, clonal, organisms. This is related to mobility in the adult phase in that mobile benthic taxa are almost exclusively unitary, whereas sessile taxa may be either unitary or modular. Although modular species are also present in the plankton (e.g. *Pyrosoma* sp., siphonophores), modular organisation appears to have particular adaptive significance for sessile species in hard substratum habitats (Hughes 1989). The indeterminate growth forms exhibited by taxa such as encrusting bryozoans, colonial ascidians, and demosponges allow efficient exploitation of space on irregular substrata and, because individual units of the organism can survive independently, modular organisation enables regeneration following levels of damage which would be lethal for unitary taxa.

These differences in adult mode have ecological implications in terms of competition for resources and the evolution of reproductive strategies in relation to habitat stability. Sessile organisms are dependent on the availability of suitable substrata for initial attachment and subsequent growth. In saturated habitats, this results in competition for space which may be manifested as overgrowth of weaker taxa by stronger spatial competitors, or by stand-offs involving chemical or physical defence mechanisms. Sessile taxa, therefore, compete for a single resource, space, which gives access to a common food resource, seston (Buss 1979, Buss & Jackson 1979, Hughes 1989, Buss 1990). Although competition for food and habitat resources may well occur between vagile taxa, it is far less straightforward to quantify and is likely to entail more complex interactions than among sessile taxa. This is primarily because the ability of individuals to move allows avoidance of competition, and a range of feeding modes and body sizes allow exploitation of different niches within the same habitat. For these reasons, competitive interactions among sessile taxa are likely to be more deterministic than is the case for vagile taxa and the probability of local extinction is consequently higher. This in turn suggests that dispersal at some point in the life cycle is imperative for sessile taxa but may be of lesser importance in vagile taxa.

Larvae

The life histories of a majority of marine benthic macrofauna species involve a morphologically distinct larval phase which precedes metamorphosis into the adult form (Thorson 1950, Mileikovsky 1971, Chia 1974, Pechenik 1999). The prevalence of larval development suggests that the larval phase is of significance in terms of life history adaptations to a benthic existence. Within the broad definition of larval development, however, there is considerable variability in trophic mode, behaviour, and duration. Several schemes of classification have been devised to categorise the range of larval types (e.g. Thorson 1950, Chia 1974, Jablonski & Lutz 1983, Levin & Bridges 1995, Poulin et al. 2001) but all are based primarily on trophic mode (feeding or non-feeding), and behaviour (pelagic or benthic). Planktotrophic larvae feed in the plankton during development and have pelagic lives which may extend from less than one week in some species up to months in others. Lecithotropic larvae possess yolk reserves sufficient for development, are typically shorter-lived and may be either pelagic or benthic in habit. In addition to these categories, however, some species exhibit mixed life histories in which a period of development in either a benthic egg-capsule or parental brood-chamber precedes a pelagic larval phase. Still others have demersal, non-planktonic larvae. Further complexity is added by the ability of some lecithotropic larvae to exhibit facultative planktotrophy (McEdward 1997) and that there can be considerable intraspecific variation in the duration of the larval phase (Gee 1963, Hadfield & Strathmann 1996). It is also significant in terms of the selective advantages of larval development that direct development, in which there is no free-living larval stage, is by no means uncommon.

In some taxa, the relative occurrence of pelagic and benthic development modes shows broad trends associated with habitat type. This suggests that any selective advantage of larval type is dependent to some degree on environmental factors. Working primarily with prosobranch molluscs, Thorson (1950) identified both a latitudinal gradient, in which pelagic larvae become progressively less common towards the poles, and a depth gradient in which pelagic larvae become less common with increasing depth (Thorson's Rule, Mileikovsky 1971). He explained both gradients in terms of two factors: the availability of planktonic food, and the effects of low temperature on development. Phytoplankton blooms are brief at high latitudes because of seasonal light limitation

(Clarke & Leakey 1996), and are absent from the deep-sea below the photic zone because of light attenuation with depth. In this context the extended larval development times associated with low temperatures (Hoegh-Guldberg & Pearse 1995) are apparently incompatible with the short period of food availability. Thorson concluded, therefore, that pelagic larvae are selected against in these environments because of food limitation and increased mortality from predation during extended planktonic development.

It has become increasingly apparent, however, that these broad-scale patterns do not hold true for all taxa and that species with pelagic larval development and species with direct or benthic larval development coexist in most habitats. Indeed, Thorson himself was aware of conspicuous exceptions to these general patterns (e.g. Thorson 1950, p23). It is of particular interest here that the two regions identified by Thorson (1950) as selecting strongly against pelagic larval development, polar seas and the abyssal depths, are now known to contain many species with pelagic larvae. In the Antarctic, pelagic larvae, particularly lecithotropic larvae, are more widespread than was previously believed (Pearse et al. 1991b, Stanwell-Smith et al. 1999) and some of the most abundant benthic species have long-lived planktotrophic larvae which persist through winter (Bosch et al. 1987, Bosch & Pearse 1990, Poulin et al. 2002, Pearse & Lockhart 2004). Similarly, pelagic larvae are found in the life cycles of many deep-sea benthic invertebrates (Rex & Waren 1982, Tunnicliffe 1991, Tyler & Young 2003).

Many approaches have been used to predict favoured modes of reproduction in varying habitats, most of these based largely on the relative metabolic and ecological costs of larval and non-larval development (e.g. Vance 1973b, a, Crisp 1974, McEdward 1997, Reitzel et al. 2004). However, most results have proved either equivocal or inadequate to explain observed patterns of distribution (Underwood 1974; Grahame and Branch 1985; Strathmann 1985). The emerging picture, therefore, is one of considerably more variability, both in large-scale patterns of developmental mode and in the life cycles of individual species (Hadfield & Strathmann 1996) than is suggested by simple models and the earlier paradigms.

Adaptive significance of larval development

The principal advantages of a pelagic larval phase are thought to be the capacity for dispersal and exploitation of phytoplankton blooms in the upper water-column. The suggested drawbacks of a pelagic larval phase include exposure to predation pressure in

the plankton and uncertainties associated with transient benthic food-supplies and patchy distribution of suitable settlement substrata (reviewed by Chia 1974, Pechenik 1999). Non-pelagic development, by contrast, allows the exploitation of stable local environments, does not depend on external food availability, avoids the high rates of predation which are thought to occur during the planktonic phase (Thorson 1950, Mileikovsky 1971, Chia 1974, Graham & Branch 1985), and may confer advantages for modular, sessile, species in terms of reproductive success and the pre-emption of substratum space (Jackson 1986, Hughes 1989, McKinney & Jackson 1989). Several studies have questioned the assumption of high mortality in the plankton (Morgan 1995a, Strathmann 1996, Van Dover et al. 2001, Johnson & Shanks 2003) but dispersal, feeding, and fundamental differences in body plan remain central to understanding the adaptive significance of larval development.

The ability of a species to disperse is of fundamental importance to its continued existence in the context of local short-term habitat fluctuation (Southwood et al. 1974). There is also compelling theoretical evidence that dispersal may retain great adaptive importance even in saturated, uniform and predictable environments (Hamilton & May 1977). Furthermore, there are long-term evolutionary advantages to be gained through the capacity for dispersal associated with larval development: the fossil record shows that invertebrate groups with dispersive larvae have broader distributions, exhibit lower levels of speciation and are less susceptible to extinction than are comparable groups with direct development (Jablonski & Lutz 1983, Strathmann 1985, Wray & Raff 1991). However, this implies species-level selection resulting from episodes of major climatic or geologic change. Such events are infrequent and during intervening periods of relative habitat stability, selective pressures may act in favour of direct development or short dispersal larvae (Bhaud & Duchene 1996, McEdward & Janies 1997). The relative rarity of direct development might, therefore, be due to negative macro-evolutionary consequences of brooding rather than to any advantages of planktonic larval development.

Although dispersal would seem to represent a significant advantage of larval development for benthic organisms in the majority of habitats, there are alternative explanations. Todd and Doyle (1981) have suggested that larval development arises from the necessity to co-ordinate an optimum spawning-time with a temporally limited food

supply for juveniles where these are separated by an extended period. Dispersal here is seen as being an incidental consequence of selective pressures acting on the timing of spawning and settlement rather than on the larval phase itself. Similarly, Palmer and Strathmann (1981) modelled the consequences of dispersal in varying environments and concluded that little or no advantage is gained from increased scale of dispersal. Strathmann (1985), developed this view, suggesting that although dispersal has profound evolutionary consequences in terms of gene flow, speciation, extinction and adaptation to local conditions, it is not selection for dispersal itself that maintains a feeding larval stage in life histories. Rather, a combination of trade-offs between investment per offspring, rates of development and risk in varying habitats on the one hand, and evolutionarily conservative traits in both larva and adult on the other, interact to determine development type. It has also been suggested that the pelagic larval phase is an evolutionary adaptation to avoid niche competition with, and predation from, benthic meiofauna (Warwick et al. 1986). In this hypothesis, benthic macrofauna migrate into the plankton during early development when body size is within the range of meiofauna, but settle to the benthos when body size approaches that of holoplankton. Thus, avoidance of predation and competition for food resources, first in the benthos and then in the plankton, is seen as the driving force underlying the larval phase and dispersal is again a secondary consequence. Interestingly, both Warwick et al. (1986) and Strathman (1985) imply that mortality is lower in the plankton than in the benthos for early developmental stages.

Overall, no simple rules appear to explain the observed occurrence of larval and non-larval development and the adaptive significance of the different larval modes remains obscure. Dispersal is a significant consequence of larval development for sessile benthic invertebrates, especially in patchy or transient habitats and over evolutionary time. However, whether this is the adaptive reason for the persistence of larval development is questionable. As a broad spectrum of developmental strategies evidently occurs in benthic assemblages at all latitudes and depths, it may be that competitive interactions, temporal patchiness of food resources, geological or climatic history, and limitations resulting from evolutionarily conservative physiological traits are as significant to the present ubiquity of larvae as are any adaptive advantages conferred by larval development itself.

ANTARCTIC MARINE ENVIRONMENTS

Physical characteristics & shallow biota

Antarctic seas are characterised by extremely low and stable seawater temperatures (below or near to 0°C year-round) and are subject to highly seasonal light regimes which are made more extreme in coastal marine environments by winter ice cover. Consequently, primary productivity in these waters is almost exclusively restricted to the summer months but blooms may be intense, particularly when associated with the breakout of winter fast-ice (Savidge et al. 1996, Arrigo et al. 1998, Smith et al. 1998). The rapid growth of such blooms results in a large proportion of total primary production sedimenting directly to the seabed (Honjo 1990, Bienfang & Ziemann 1992, Clarke & Leakey 1996), where it supports a diverse and abundant benthic fauna (Arntz et al. 1994, Brey et al. 1994, Clarke 1996, Clarke & Johnston 2003). The benthos, therefore, constitutes a major component of the Antarctic nearshore marine ecosystem in terms of secondary production and biomass (Brey & Gerdes 1997, Gili & Coma 1998, Gili et al. 2001).

The freezing of surface waters in winter (fast ice), and physical disturbance of the seabed by floating ice during summer, have major effects on the benthos (reviewed by Barnes 1999, Gutt 2001). Where fast ice forms, the water column is well mixed and both temperature and salinity vary little to depths of ~100m. Tidally generated currents, however, may cause horizontal advection of water masses beneath the ice. In summer, by contrast, solar heating and melt water can cause pronounced thermal stratification and salinity gradients in the upper water column. As nutrients are generally in high concentration, such stratification promotes intense phytoplankton blooms. The impacts of icebergs and fragmenting fast ice in summer can cause considerable mortality of benthic fauna (Peck et al. 1999). The frequency of such impacts is dependent to a large degree on local seabed topography but in general it decreases rapidly with depth.

Sessile fauna are generally absent on exposed substrata in the intertidal and immediate sublittoral. This is presumably mainly because of high frequencies of ice scour in summer, but freezing in winter and lowered salinity in summer may also affect colonisation (Hedgpeth 1969, Barnes 1995b). In the sublittoral, there is conspicuous zonation of benthic assemblages which, again, is assumed to be a consequence of decreasing frequency of disturbance by ice (Dayton 1975, Kirkwood & Burton 1988,

Barnes 1995c, Nonato et al. 2000). In shallow waters (<~10m) substrata are often patchily colonised and dominated by encrusting coralline algae and vagile grazers. With increasing depth, diverse sessile assemblages of bryozoans, sponges, ascidians, brachiopods, and hydroids become more common, together with locally dense populations of echinoderms, polychaetes, amphipods, molluscs, pycnogonids, and other vagile taxa. Macroalgae can be present at all latitudes but are most abundant along the western Antarctic Peninsula north of the Antarctic Circle (Moe & DeLaca 1976, Wiencke 1996). Much of the deeper continental shelf that has been studied to date is covered by dense assemblages of sessile suspension feeders (Teixido et al. 2002, Gutt & Piepenburg 2003) which may be of considerable age.

Evolutionary history

High levels of endemism in some taxa (e.g. pycnogonids, isopods, bryozoans) and the almost complete absence of others (notably reptant decapods and barnacles) are conspicuous characteristics of the Antarctic marine fauna (Dayton 1990, Arntz et al. 1994, Brey et al. 1994, Clarke & Johnston 2003). This is probably a consequence of the oceanographic context of the continent which, in turn, is linked to its tectonic history. Antarctica formed during the break-up of Gondwana in the Tertiary and subsequent formation of the Southern Ocean led to biogeographic isolation and cooling. The opening of Drake Passage (25-35 Ma, Livermore et al. 2004), in particular, resulted in the formation of the Antarctic Circumpolar Current (ACC) and associated Polar Front (Figure 1.1). This circulation initiated further cooling and became an effective barrier to the exchange of planktonic biota between Antarctic continental shelf waters and the rest of the global ocean. In consequence, the shelf fauna of Antarctica are believed to have evolved largely in isolation over at least the past 20-30Myr (Clarke & Crame 1989, Clarke et al. 2004a). During this time, however, the extent of glaciation has varied considerably.

During glacial maxima, ice sheets are believed to have extended across the whole of the continental shelf and to have eradicated or displaced much of the benthic fauna. The persistence of taxa in isolated, ice-free, refugia at these times, with consequent allopatric speciation before recolonisation of shelf areas during glacial minima, has been suggested as a mechanism by which present day patterns of diversity have evolved (Clarke & Crame 1989, 1992, Poulin & Feral 1996, Poulin et al. 2002). It is significant, in relation

to the prevalence of non-planktotrophic larval development in some clades today, that primary production in continental shelf areas was probably negligible during glacial maxima because of the absence of light under permanent ice shelves. These conditions would perhaps have selected strongly against planktotrophic larvae and favoured lecithotropic development with restricted dispersal. Subsequent recolonisation of the continental shelf following retreat of the ice shelves might, therefore, have been largely by lineages with lecithotropic development. The composition of the present benthic fauna, therefore, might be expected to reflect past selection for non-planktotrophic development. Considering the stability of the region in recent evolutionary history, however, individual species would also be expected to exhibit physiological and life history adaptations to conditions in the present interglacial: an extremely cold but thermally stable environment in which primary production is predictable but highly seasonal.

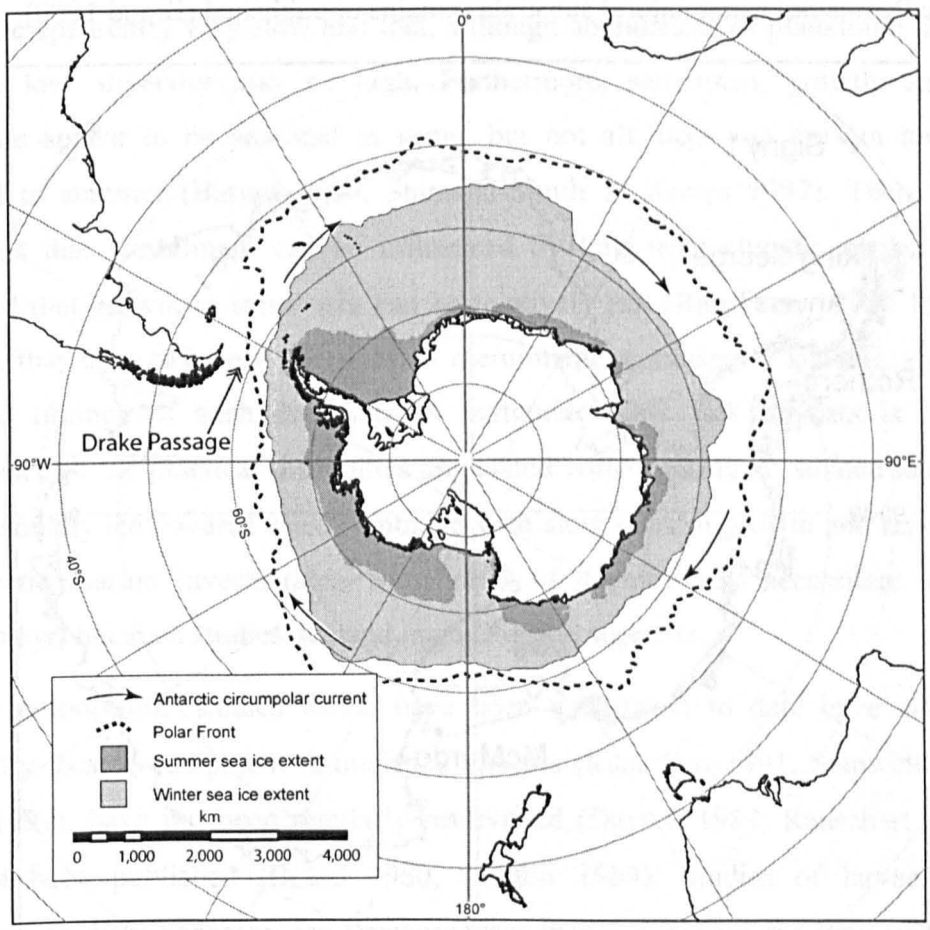


Figure 1.1 Antarctica, showing Drake Passage and approximate positions of the Polar Front, the Antarctic Circumpolar Current and the seasonal extent of sea ice.

Studies of benthic colonisation and larval ecology in the Antarctic

Benthic nearshore assemblages at several Antarctic locations have been described in detail (Dayton et al. 1974, Kirkwood & Burton 1988, Barnes 1995c, Nonato et al. 2000, Barnes & Brockington 2003) but there have been few studies of benthic recruitment, growth, or larval ecology. Colonisation data have been published from work at McMurdo Sound (Dayton 1989, Pearse & Pearse 1991), King George Island (Rauschert 1991) and Signy Island (Barnes 1996, Stanwell-Smith & Barnes 1997) (Figure 1.2). However, only the latter study (Stanwell-Smith & Barnes 1997) reports quantitative data on seasonal variations in recruitment and assemblage growth. The others provide only brief, non-quantitative, descriptions of assemblages after 1 year (Pearse & Pearse 1991), 3 years (Rauschert 1991), or 5 and 10 years (Dayton 1989). In addition, a 3-year colonisation study at Davis Station (Figure 1.2) has yet to be published (Australian Antarctic Division, J. Stark personal communication) and a 1-year study at Anvers Island (west Antarctic Peninsula) using natural substrata remains unpublished (Brand 1980).

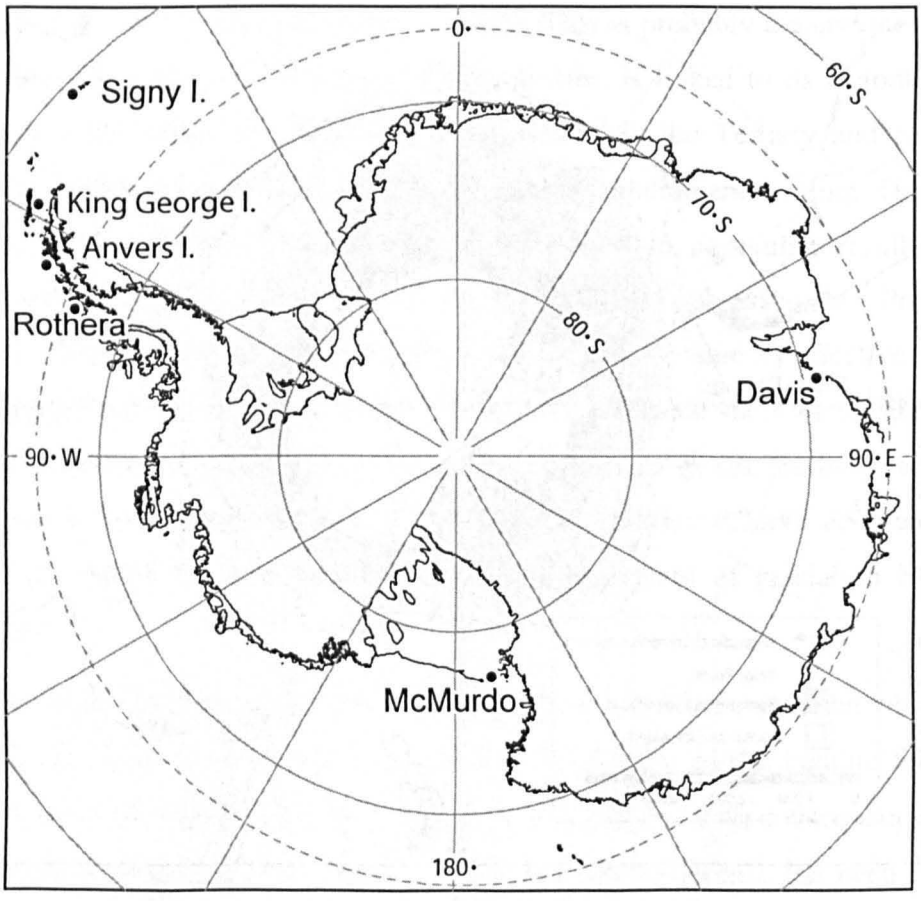


Figure 1.2 Locations of previous studies in benthic colonisation and larval ecology in Antarctica. Dashed line indicates the Antarctic Circle.

The only published year-round study of planktonic larvae of benthic invertebrates in the Antarctic is from Signy island (Stanwell-Smith et al. 1999) but another unpublished study from Davis station (Kirkwood 1994) details seasonal abundances of echinoderm and ascidian larvae over 2 years in Ellis Fjord. In addition, several short-term (days-weeks) studies provide varying amounts of detail on the occurrence of meroplanktonic larvae from a number of locations around the continent. These include McMurdo Sound (Pearse & Bosch 1986, Bosch et al. 1987, Foster 1987, 1989, Knox et al. 1996, Sewell 2005), the West Antarctic Peninsula region (Scheltema et al. 1997, Absher et al. 2003), the Bellingshausen Sea (Shreeve & Hayward 1995, Shreeve & Peck 1995), Adelie Land (Bhaud et al. 1999), the Weddell Sea (Hain & Arnaud 1992), and the Kerguelen archipelago (Bhaud et al. 1999).

These colonisation and larval studies are discussed in more detail in the relevant chapters later in the thesis. The general points to emerge, however, are that rates of settlement and growth are apparently very slow and that, although abundances of planktonic larvae are generally low, diversity may be high. Furthermore, settlement, growth, and larval occurrence appear to be seasonal in some, but not all, taxa and are not necessarily restricted to summer (Barnes 1996, Stanwell-Smith & Barnes 1997). There are also indications that recruitment can be influenced by long-term climatic cycles (Dayton 1989) and that growth in some taxa can be relatively fast (Rauschert 1991). It is clear, however, that there are very few data on recruitment processes in general, and on the rates and timings of such processes in particular. This lack of data is largely a consequence of the practical difficulties associated with working at isolated locations in cold, seasonally ice-covered seas, combined with slow rates of growth and reproduction in Antarctic marine invertebrates. Slow rates of development necessitate long-term studies (>1yr) but such studies demand major logistic support.

The few colonisation studies which have been undertaken to date have either been affected by loss of equipment through ice impacts (Rauschert 1991, Stanwell-Smith & Barnes 1997), have not been regularly resurveyed (Dayton 1989, Rauschert 1991), or have not been published (Brand 1980, Dayton 1989). Studies of larvae are less susceptible to disturbance by ice (because gear is not deployed for long periods) but labour-intensive sample processing, differences in methodology between studies, and

difficulties with identification, have resulted in sparse data and problems with making reliable comparisons between data sets.

AIMS OF THE PRESENT STUDY

In the context of generally very limited knowledge of colonisation processes in the Antarctic, the overall objective of the present study was to produce the most thorough study of benthic colonisation processes yet undertaken. By incorporating simultaneous measurements of short-term recruitment to the seabed, development and growth of assemblages following settlement, and the abundance and diversity of larvae in the water column, the project aimed to develop a general picture of the principal factors controlling the establishment and maintenance of assemblages in the region. More specifically, the following questions were addressed:

- Are pre-settlement or post-settlement factors more important in structuring assemblages?
- What influence does environmental seasonality have on the timing of recruitment and growth?
- Does reproductive mode show specific adaptations to the Antarctic near-shore marine environment?

The first question is concerned with the relative influence of variations in the number and diversity of settling larvae, on the one hand, and subsequent mortality on the other. Previous studies at Signy Island (Stanwell-Smith & Barnes 1997) and McMurdo Sound (Dayton 1989) suggest that recruitment limitation can be a significant factor in the establishment of assemblages but the data are inconclusive.

The second question relates to the expectation that both recruitment and growth will be constrained to occur during the summer period of maximum food availability. Growth is highly seasonal in some vagile taxa (Brockington et al. 2001, Fraser et al. 2002a, Clarke et al. 2004b) but few data are available for sessile taxa (Barnes 1995a). The only existing study of seasonality of recruitment (Stanwell-Smith & Barnes 1997) suggests that recruitment in some sessile groups might be aseasonal.

The third question follows from the debate about the adaptive significance of larval type in relation to environment, which is discussed above. The intense seasonality and the

prevalence of ice-mediated disturbance over evolutionary timescales in Antarctic seas suggests that, if there are strong selective pressures acting on the larval phase, they are most likely to be apparent here.

These are, clearly, broad objectives which were unlikely to be answered definitively with the time and resources available here. However, as the project was the first of its kind in the region, it was anticipated from the outset that it would serve largely to indicate directions for more detailed research in the future.

Chapter 2 – The study area

Chapter 2 – The study area

GENERAL CHARACTERISTICS

All research described in this thesis was carried out from the British Antarctic Survey research station at Rothera Point on the southeast coast of Adelaide Island, west Antarctic Peninsula (67° 34.5′ S, 68° 07.0′ W, Figure 2.1). The hydrography, circulation dynamics, and productivity of the region are the subject of long-term studies by both the Southern Ocean Global Ecosystems Dynamics (SO GLOBEC) and Palmer Long Term Ecological Research (Palmer LTER) projects. Detailed descriptions of large and medium scale processes in the surrounding continental shelf area are available in the published output of these projects (e.g. Smith 1999, Hofmann et al. 2004, and associated references) and in Meredith et al. (2004).

Water movements around Rothera Point are influenced by a complex semidiurnal tidal regime (~2 m maximum range, Proudman Oceanographic Laboratory, unpublished data) which causes an oscillatory circulation within Ryder Bay and predominantly SSE currents in Laubeuf Fjord (Figure 2.1). Off-shore transport of surface waters caused by the prevailing northerly winds, together with circulation of water masses on the continental shelf and intrusions of Circumpolar Deep Water (CDW) (Klinck et al. 2004, Prezelin et al. 2004) are likely to influence primary productivity and the transport of pelagic larvae through vertical-mixing and advection. Larger scale circulations, and intrusions of CDW in particular, might be expected to cause interannual variability in planktonic and benthic production through changes in nutrient fluxes to coastal areas (Garibotti et al. 2003, Meredith et al. 2004, Prezelin et al. 2004). Seabed topography in the area is heterogeneous at all scales but in general reflects the mountainous terrestrial environment, with steep rocky substrata descending to depths of >500m within 1km of the shore in many places. Areas of soft sediments are rare within SCUBA working depths (<50 m) but to the north of Rothera Point the seabed shelves gently and consists of densely-packed rock fragments overlain by fine glacial till.

Routine year-round measurements of seawater temperature, salinity, down-welling light, dissolved nutrients, and concentrations of phytoplankton photosynthetic pigments have been made in Ryder Bay since 1997 (Rothera oceanographic Time Series (RaTS), British Antarctic Survey unpublished data). All physical and biological parameters show strong

seasonality, following changes in insolation through the year. The maximum annual temperature range at 15 m is small (<4°C) but shows clear seasonality (Figure 2.2). Primary productivity exhibits major changes in magnitude through the year with intense summer blooms typically lasting for only a few weeks, although there may be distinct successive blooms within a single summer (Figure 2.2). By comparison with the summer, primary productivity in winter is negligible but a low level of production by nano- and pico-planktonic cells continues through most of the year, as at other Antarctic locations (Clarke & Leakey 1996).

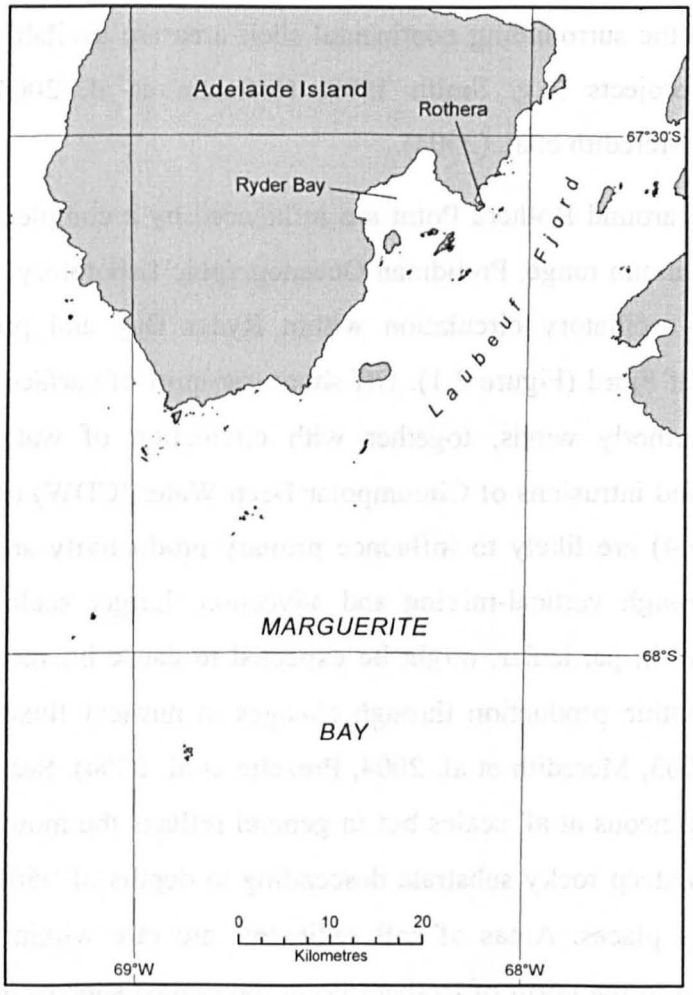


Figure 2.1 The northern part of Marguerite Bay, showing Adelaide Island, Ryder Bay, and Rothera Point.

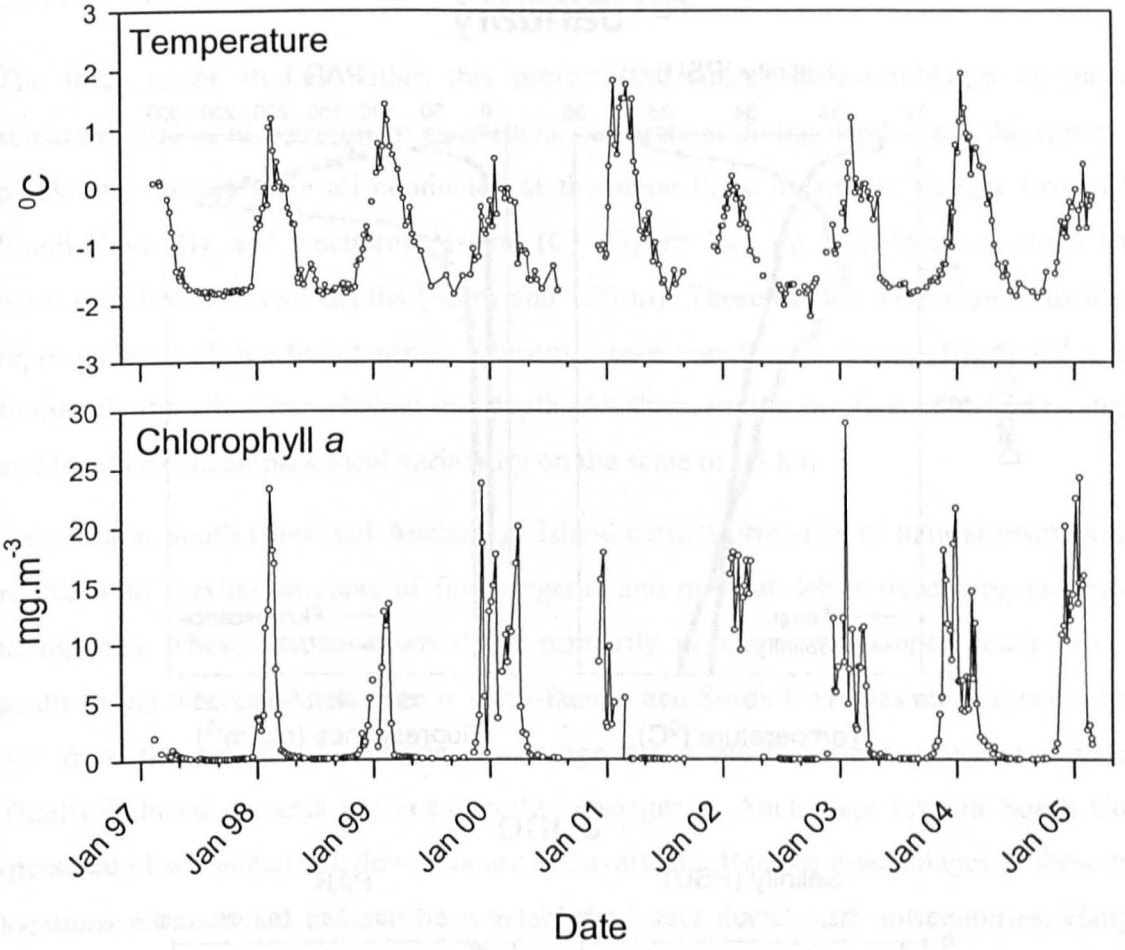


Figure 2.2 Seawater temperatures and total chlorophyll *a* concentrations at 15m depth in Ryder Bay from February 1997 to February 2005. Rothera oceanographic Time Series (RaTS), British Antarctic Survey unpublished data.

In summer, the upper layers of the water column are warmed by insolation (down to ~10-15 m) and salinity is reduced by melting ice (Figure 2.3). In calm weather, this may lead to formation of distinct thermo- and pycnoclines and intense phytoplankton blooms above ~30 m depth. The most intense blooms are associated with the initial breakout of winter fast-ice and result in large fluxes of phytoplankton cells to the seabed (personal observation). When sea-ice forms in winter, the water column is well-mixed, temperature and salinity are uniform down to ~50 m, and primary production is negligible (Figure 2.3). In the southern part of Laubeuf Fjord and Ryder Bay, however, persistent sea-ice does not form in every winter. The proximate cause of this is the prevailing strong offshore wind which brings warmer air from the north. The ultimate causes, however, are likely to be large-scale hydrographic and atmospheric processes (Murphy et al. 1995, Meredith et al. 2004).

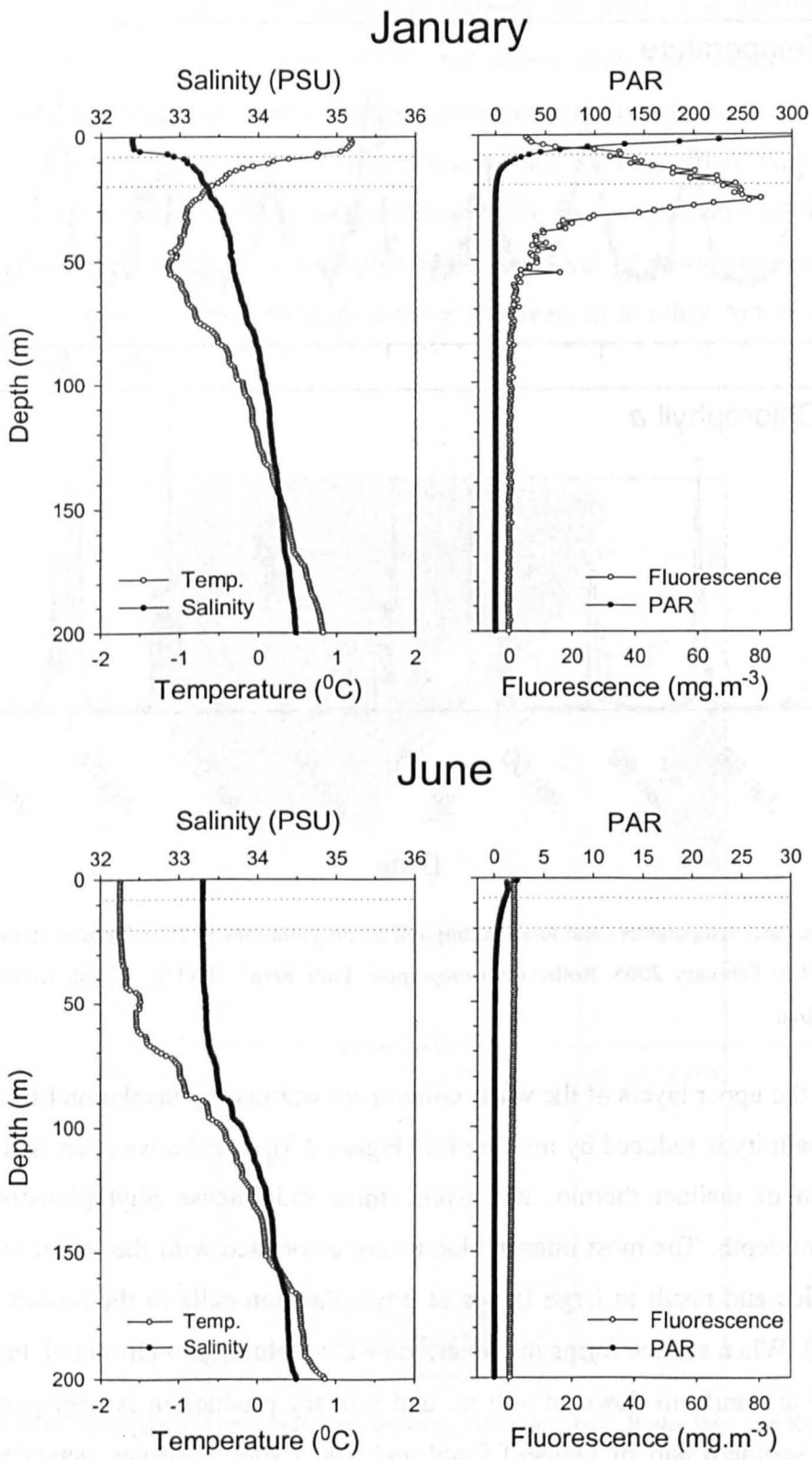


Figure 2.3 Ryder Bay: water column profiles in summer (January, upper panel) and winter (June, lower panels), showing salinity, temperature, intensity of photosynthetically active radiation (PAR), and fluorescence as a measure of photosynthetic pigment concentrations. Dotted lines indicate the depths at which the present study was conducted (8m and 20m). (RaTS, BAS unpublished data).

STUDY SITES

The three major studies within this project (the survey of assemblages on natural substrata, studies of recruitment to artificial substrata at diving depths, and the survey of planktonic larvae) were all conducted at the same three locations: Hangar Cove (A); South Cove (B), and Anchorage Island (C) (Figure 2.4). At each location, study sites were established at two depths (~8 m and ~20 m). These depths were chosen as being representative of two broad zones: a heavily ice-scoured zone above ~10 m, and a less frequently disturbed zone below this depth. All three studies are thus stratified by depth and locations encompass local variability on the scale of ~5 km.

Substrata at South Cove and Anchorage Island consist primarily of natural bedrock and rubble with varying amounts of fine biogenic and mineral debris depending on seabed topography. These two locations differ primarily in aspect and slope: South Cove is south-facing whereas Anchorage is north-facing, and South Cove has an incline of about 30° from the horizontal whereas Anchorage has a much steeper, irregular drop-off. Tidally induced currents are considerably stronger at Anchorage than in South Cove (personal observation) but flow data are not available. Benthic assemblages at these two locations are assumed to have been established over decades, if not centuries. Hangar Cove contrasts with the other locations in that the hard substrata here are the boulder foundations for the Rothera airstrip, which was constructed in 1991. The boulders are of natural rock quarried from Rothera Point and the runway extends northwards, separating Hangar Cove from the rest of North Cove. The natural substratum in Hangar Cove is a gently sloping gradient of compacted rubble covered with fine sediment and currents are very slow at all states of tide.

The study locations were selected on the basis of both ecological and practical considerations. As there were no previous data on the larval ecology or colonisation of benthic assemblages in the area, a principal requirement of the present study was to generate a broadly representative picture of such processes. High-resolution sampling at a single location, therefore, was rejected in favour of covering a range of locations with differing characteristics. However, practical constraints including the accessibility of sites, the number of dives that can be accomplished routinely, the number of replicate units that can be sampled within a single dive, and the number of samples that can be

processed ashore within the requirement for monthly sampling intervals, limited the number of suitable locations.

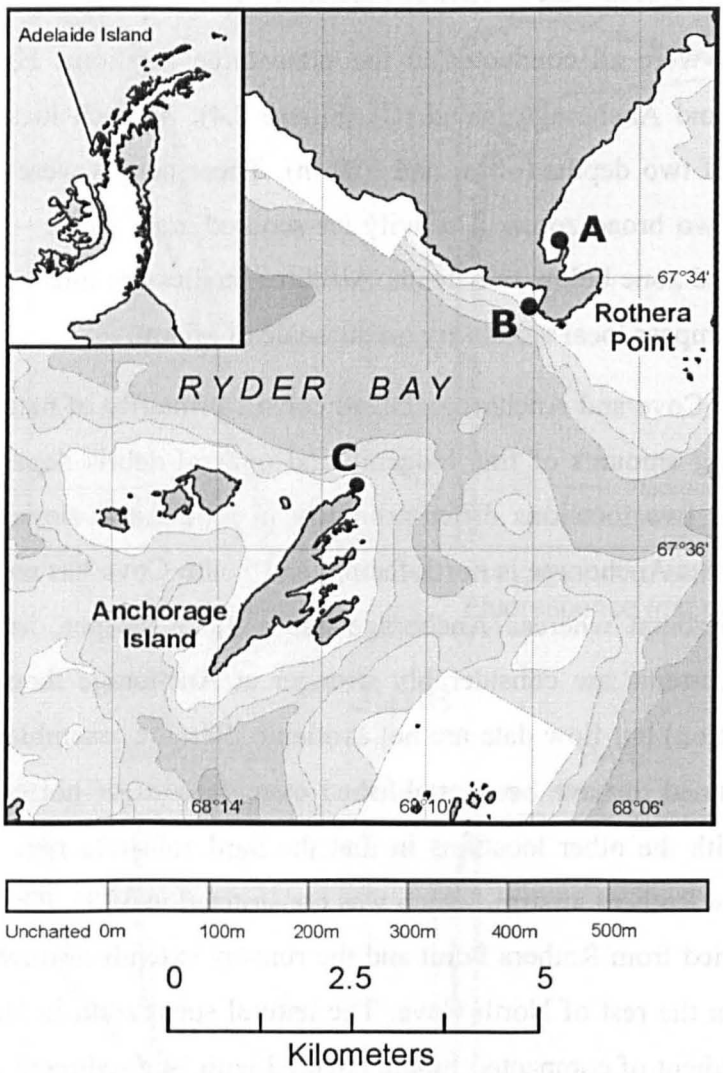


Figure 2.4 Principal locations used in studies of assemblages on natural substrata (Chapter 3), recruiting to artificial substrata (Chapters 4-6) and of planktonic larvae (Chapter 9). A, Hangar Cove; B, South Cove; C, Anchorage Island. Assemblages at 8m and 20m depths were studied at each location.

The probability of gaining year-round access was central to the selection of study locations. South Cove and Hangar Cove are readily accessible from shore in most wind and ice condition and thus were immediate choices. These are also the locations at which almost all previous marine biological work has been undertaken at Rothera, and thus provide some contextual data against which to evaluate results from the present study. However, reconnaissance dives at other locations in Ryder Bay indicated that near-

vertical rock faces descending to >80 m were common substrata in the local area and that sessile assemblages at a given depth in these habitats were often comparable to assemblages only found at somewhat greater depths in South Cove. Therefore, the location at the northern tip of Anchorage Island was included in the study to represent this habitat type. Access becomes more uncertain with increasing distance from Rothera Point and the consequent reliance on suitable sea or ice conditions for travel. It was anticipated, therefore, that the Anchorage Island sites would probably be inaccessible at some times of year.

Chapter 3 – Assemblages on natural substrata

[The data in this chapter are also presented in: Bowden DA (2005) Quantiative characterisation of shallow marine benthic assemblages at Adelaide Island, Antarctica. Marine Biology, **146 (6):** 1235-1249.]

Chapter 3 – Benthic assemblages on natural substrata

INTRODUCTION

Observations of the patterns of distribution of organisms are the basis from which ecological hypotheses are generated and subsequent testing of hypotheses is thus dependent on the accuracy of the initial description of pattern (Andrew & Mapstone 1987, Levin 1992, Underwood et al. 2000). Ideally, the initial characterization of assemblages in a region requires accurate quantitative and qualitative data to be recorded for all taxa across a broad spectrum of spatial and temporal scales. However, it is a major undertaking to sample even a small area with the resolution which would be desirable for such studies and, in consequence, individual surveys selectively sample subsets of organisms and locations within relatively narrow spatial and temporal bounds.

The particular difficulties associated with sampling benthic sublittoral biota exacerbate the problems of representative sampling of assemblages and historically our knowledge of such systems has developed by the accumulation of data from a succession of surveys, each based on relatively few grab or dredge samples targeting particular components of the biota. The advent of direct observation and sampling by divers, submersibles and remotely operated vehicles has greatly increased the scope of marine benthic studies and in combination with the development of effective underwater photographic and video systems, allows assemblages to be surveyed in finer detail and over wider spatial scales (e.g. Vevers 1952, Bohnsack 1979, Kirkwood & Burton 1988, Roberts et al. 1994, Gutt et al. 1996, Smith & Witman 1999, Teixido et al. 2002). This is particularly true of assemblages on hard substrata for which traditional techniques are inefficient (Holme & McIntyre 1984, Kennelly & Underwood 1985).

Antarctic marine benthic assemblages develop at rates many times slower than those in lower latitudes owing to slow overall growth rates (when integrated over a full year) for most taxa (Stanwell-Smith & Barnes 1997). There is a strong case, therefore, for non-destructive photographic sampling techniques to be employed when possible in these latitudes in order both to limit unnecessary disturbance to assemblages, which may have taken decades, or perhaps centuries, to reach their present state (Dayton 1989, Arntz et al. 1994, Barnes et al. 1996, Gutt et al. 1996) and to allow time-series studies to be undertaken without introducing confounding effects from earlier sampling.

Photographic techniques have their own inherent limitations, however, in that they omit, or under-sample, infaunal, cryptic, and rapidly motile species. In addition, estimates of abundance or areal cover may be subject to errors owing to variability of seabed topography and shielding from view by over-storey growth (Foster et al. 1991, Meese & Tomich 1992, Bernhardt & Griffing 2001). Furthermore, because of the dependence on the optical resolution of the imaging system employed, the scale at which photographic surveys are conducted can influence which components of the assemblages under study are detected; an effect directly analogous to the use of different sieve mesh sizes in conventional methods of benthic sampling. While the effectiveness of photographic sampling has been compared to conventional methods in several studies (McIntyre 1956, Foster et al. 1991, Meese & Tomich 1992, Roberts et al. 1994), evaluations of the effects of sampling at different photographic scales have yet to be undertaken.

The principal objective of the present survey was to characterize benthic assemblages in the study area in order to provide a valid context in which to evaluate data from the studies of invertebrate larval diversity, settlement, and early assemblage development. The wide scope of these studies required that the survey should estimate benthos components with distributions spanning a range of scales from small-scale encrusting biota, requiring examination at the scale of square millimetres, up to large unitary macrofauna distributed at scales of square metres. To accommodate this range of scales, a strategy based on non-destructive photographic sampling at two spatial scales was employed, with the addition of a conventional physical sampling element to evaluate cryptic epifaunal assemblages. The simultaneous use of two scales of photographic sampling allowed quantitative and qualitative comparisons to be made of the effectiveness of each scale at detecting different elements of the assemblages under study. This paper is intended both as a presentation of ecological data from the survey and as an evaluation of the methods used.

METHODS

Survey sites

Sampling was conducted at the study sites selected for both the settlement plate and planktonic larvae studies (Chapter 2). Thus, benthic assemblages were surveyed at two

depths (8 m and 20 m) at each of the 3 locations (Hangar Cove, South Cove, and Anchorage Island).

Photographic surveys

Photographic surveys of the seabed at 8m and 20m depths were undertaken during the austral winter 2002 by divers using SCUBA equipment. At each depth, at each location, surveys were conducted using two different frame sizes: 0.015 m^2 and 0.32 m^2. A Nikonos V 35 mm camera with UW Nikkor 28 mm lens and ISO 50 colour reversal film was used throughout. For the 0.015 m^2 survey, cameras were fitted with a Nikonos close-up lens and frame to which insulating-tape guides were attached to demarcate a central 0.015 m^2 analysis area. For the 0.32 m^2 survey, an 800 mm distance probe ensured repeatable camera distance from the substratum and hence consistent framed area. A 10 cm square opaque Perspex plate was fitted to the distal end of the probe to carry image identification data (date, site, depth) and to allow accurate image calibration during later analysis. Lighting was by one (0.015 m^2 quadrats) or two (0.32 m^2 quadrats) Nikonos SB105 flash units fitted with diffusers.

At each survey site photographs were taken at intervals along the selected isobath. Subjective selection was minimised by placing and firing the camera with eyes closed. For the 0.32 m^2 survey, spacing between images was gauged as one fin stoke (~1 m). For the 0.015 m^2 survey 5 images were taken between each fin stroke. A total of eighteen 0.32 m^2 images, and thirty-five 0.015 m^2 images were taken at each depth at each location, resulting in transect distances of approximately 18 m and 7 m for the 0.32 m^2 and 0.015 m^2 surveys respectively. For comparison of the effectiveness of sampling at different scales, post-sampling effort was standardized by selecting equal numbers of images at each scale for analysis. Fourteen images at each scale from each site were selected at random, resulting in total areas analysed per depth, per location, of 4.48 m^2 and 0.21 m^2 for the 0.32 m^2 and the 0.015 m^2 surveys respectively. The total areas analysed across both depths and all locations were thus 26.88 m^2 and 1.26 m^2 respectively.

Image analysis

Transparencies were scanned (Nikon LS 2000) at a resolution of 600 dpi and an output image size of 2400 x 1600 pixels. Image analysis for sessile organisms followed the "interactive colour segmentation" method described by Bernhardt and Griffing (2001)

using *Adobe Photoshop 5.5* (Adobe Systems Incorporated, San Jose, CA) and the freeware image analysis program, *ImageJ* (http://rsbweb.nih.gov/ij/). Counts of vagile fauna were made by eye, using the "crosshair" tool in *ImageJ*.

All taxa discernible in the images were identified to the lowest taxonomic level possible. Sessile taxa, both fauna and algae, were quantified as percentage areas covered, whereas mobile taxa were recorded as counts of individuals. Only slow-moving mobile taxa were recorded (referred to here as 'vagile' taxa) as highly mobile taxa such as fish and crustaceans were poorly sampled by the methods used. All area measurements were taken as two-dimensional projected areas at the film plane and no attempt was made to adjust for perspective or parallax differences caused by variations in seabed topography.

Collected rocks survey

In order to assess assemblages of cryptic encrusting taxa, rocks were collected by divers from each of the survey sites. Two collecting points approximately 3m apart were established at the relevant depth and from each a single bucket was filled with rocks. There were no criteria as to rock size or number. Rocks were dried at room temperature, labelled by site, depth and collecting point, and individually numbered. Ten rocks from each sample were then selected at random for analysis. Thus, 20 rocks were examined for each depth/location combination and 120 rocks in total.

To derive percentage cover data, it was necessary to calculate rock surface areas. Each rock was weighed and a random sample of 20 were immersed individually in water in a graduated flask to measure their volumes. From these figures a regression of rock weight against volume (r^2 = 0.997) gave a value for mean rock density and hence allowed calculation of volume for each rock. Approximate surface area was then calculated by multiplying the area of the prism enclosing each rock by its prismatic coefficient, C_p (Eqn. 1, where V is volume and x,y,z are the principal dimensions of the enclosing prism)

$$C_p = \frac{V}{xyz} \qquad \text{Equation. 3.1}$$

Surface areas of a random sample of 12 rocks were then measured as accurately as possible, using squared paper, and a regression of their measured areas against calculated areas (Calc.Area = 0.883 x measured area, r^2 = 0.983) was used to derive a constant by which initial calculated areas were divided to give the adjusted surface areas used in all

analyses. To check that there were no gross discrepancies in the size distribution or total surface area of rocks analysed at each site, an ANOVA with Location, Depth and Sample as main factors was performed on the calculated area values following $\log_{10}$ transformation to normalize variances.

All encrusting fauna on the rocks were identified to the lowest taxonomic level possible, in most cases to species. Areal coverage of modular encrusting taxa was assessed by means of a template marked with a ten-stage doubling scale of circular areas ranging from 5 mm^2 up to 2560 mm^2. Spirorbid polychaetes were counted and their areal coverage estimated by multiplying abundance values by a standard area-per-individual. Serpulid polychaete areal coverage was estimated by recording overall length and assuming mean width to be 1 mm.

Data analysis

Data from each survey scale were examined separately. To assess the effectiveness of sampling at each scale, species accumulation curves were produced for 8 m and 20 m depth categories. Abundance counts for unitary organisms were standardized to number of individuals per square metre, and areal coverage values for encrusting fauna and algae were expressed as percentage cover of the sample area (i.e. of 0.32 m^2, 0.015 m^2, or calculated area of individual rocks). For the highly abundant species, *Sterechinus neumayeri* and *Nacella concinna*, differences in population density between depths and locations were tested for significant differences by factorial ANOVA, following appropriate transformation of the data to standardize variances. All abundance and area values in the text are given as the mean ± 1 standard error.

Multivariate analyses were conducted using routines within the PRIMER statistical package (Primer-e Ltd. Plymouth, UK). In all analyses the survey locations and depths defined above were used as main factors. Preliminary analyses of all taxa combined were conducted on presence/absence data to allow combination of area and count data. Subsequent analyses at each scale were performed on motile and sessile biota groups separately, using fourth-root transformed data to allow comparison of quantitative data whilst down-weighting the influence of highly abundant taxa.

For each analysis, datasets were first examined by MDS (multidimensional scaling) ordinations of a matrix of Bray-Curtis similarities between samples. Differences between depth and location groupings were then tested using two-way crossed analysis of

similarity (ANOSIM) and, where Global R values were significant, pairwise comparisons between locations at each depth were performed (Clarke & Warwick 2001). Percentage similarities and dissimilarities between samples from different depths and locations, together with rankings of species contributions to them, were then calculated using the Similarities Percentage (SIMPER) routine. A cut-off point of 75% of total dissimilarity between groups was used and the ratio of the average dissimilarity contribution of each species to the standard deviation (Dissim/SD) was used as a guide to which species contributed most consistently to differences between groups across all samples. If the contribution of a species to dissimilarity between, say, depth groups is consistent across all sample comparisons, the standard deviation will be low and the ratio Dissim/SD will be large, whereas, if that species' contribution to dissimilarity between depths is high at only one location, the corresponding standard deviation will be high and the resulting Dissim./SD ratio small.

RESULTS

Overall

A total of 79 faunal taxa, representing 18 classes and 10 phyla, together with 6 algal taxa, were recorded (Table 3.1). None of the three survey scales, by itself, encompassed the full range of taxa recorded in the survey overall. The two photographic survey scales yielded very similar taxonomic profiles, but the larger scale (0.32 m^2) detected more widely-dispersed, low abundance species, particularly echinoderms. The resolution of the larger images was also sufficiently fine to detect and identify organisms as small as ~10mm in diameter, resulting in considerable overlap with the smaller scale images. Changes in the set of taxa identified at each scale may be attributed to both the scale of observation and the total area surveyed. Thus, all bryozoan species were readily identifiable under microscopic examination of rocks but only those few with particularly distinctive macroscopic colony form, such as *Beania erecta*, could be discriminated in photographs. In contrast, more echinoderm species, which were easily identifiable at both photographic scales, were recorded in the 0.32 m^2 scale survey than in the smaller quadrats, presumably owing to the greater total area of substratum covered at the larger scale.

Species accumulation curves for 8 m and 20 m depths (across all three locations) suggest that the majority of species detectable with the techniques used were probably sampled (Figure 3.1). The gradients of curves for the two photographic scales at both depths, however, are still rising after 42 samples suggesting that more species remain unsampled at these scales than at the scale of individual rocks. The set of taxa identified differed with sampling scale but there was overlap across all three scales (table 1) and at each sampling scale there was a subset of species which were either detected, or were quantifiable, only at that scale (Figure 3.2). At the largest scale (0.32 m^2 quadrats), there were fifteen such species from six phyla; at the intermediate scale (0.015 m^2 quadrats) there were twelve species from five phyla, and at the smallest scale (individual rocks) there were twenty species from a single phylum. Of these 'unique' species sets, the two photographic scales showed a marked bias in the type of organism detected: at the larger scale two-thirds of these species were vagile, whereas at the smaller scale two-thirds were sessile.

At all scales, for full datasets and both vagile and sessile components, multivariate analyses detected significant differences between assemblages at 8m and 20m depths (Table 2). Higher ANOSIM R values indicate that these differences were most pronounced for sessile assemblages at the two photographic survey scales but that there was less distinction between depths for sessile assemblages on collected rocks. MDS ordinations (Figure 3.3) and pairwise ANOSIM comparisons between locations (Table 3) show assemblages at Hangar Cove sites to be markedly different from those at either South Cove or Anchorage; ANOSIM R values being substantially higher for all comparisons involving Hangar Cove. MDS ordinations and ANOSIM R values also indicate that the dissimilarities between Hangar Cove assemblages and those at other locations are greater at 20 m than at 8 m.

Table 3.1 Full taxon list with indication (•) of surveys in which each was recorded.

Phylum	Class	Order	Family/Genus - species	0.32m2	150cm2	Rock
Porifera	Demospongiae		*Dendrilla antarctica*	•	•	
			indet sponge 1. (yellow, smooth)		•	
			indet sponge 2. (white)	•	•	•
			indet sponge 3. (orange)	•	•	
			Kirkpatrickia variolosa		•	
			Sphaerotylus antarcticus	•	•	
			Tetilla leptoderma		•	
Cnidaria	Anthozoa	Alcyonacea	*Alcyonium antarcticum*	•	•	•
			Clavularia frankliniana	•		
			Primnoella sp.	•		
			Urticinopsis antarctica	•	•	
	Hydrozoa	Leptothecata	Hydroids - bush form	•	•	
			Aglaopheniidae	•		
			Tubullariidae		•	
Nemertea	Anopla	Heteronemertea	*Parborlasia corrugatus*	•		
Annelida	Polychaeta		Sabellidae (Potamilla antarctica)		•	
			Serpulidae	•	•	•
			Spirorbidae		•	•
			Flabelligera mundata		•	
			Terebellidae	•	•	
Mollusca	Gastropoda	Docoglossida	*Nacella concinna*	•	•	
			Iothia coppingeri	•	•	
			Margarella sp.		•	
		Nudibranchia	*Austrodoris kerguelensis*	•		
			Tritoniella belli			
			Eubranchus sp?	•	•	
			Tritonia antarctica	•		
			Noteaolidia sp.		•	
		Lamellariida	*Marseniopsis mollis*	•		
	Polyplacophora		Chitons		•	
	Bivalvia		*Adacnarca nitens*			•
Bryozoa	Stenolaemata	Cyclostomatida	Cyclostome bryozoans		•	•
	Gymnolaemata	Cheilostomatida	Bryozoans - encrusting indet.	•	•	
			Beania erecta	•	•	•
			Bryozoans - erect indet.	•	•	
Brachiopoda	Articulata	Terebratulida	*Liothyrella uva antarctica*	•	•	
Echinodermata	Asteroidea	Phanerozonida	*Odontaster validus*	•	•	
			Odontaster meridionalis	•		
			Perknaster aurorae	•		
			Porania antarctica	•		
			Notasterias sp.	•	•	
		Forcipulatida	*Lophaster* sp.	•	•	
			Diplasterias brucei	•	•	
			Cryptasterias tarqueti	•	•	
			Porania antarctica glabra	•	•	
			Indet asteroids (juvenile indet.)	•	•	
	Echinoidea	Echinoida	*Sterechinus neumayeri*	•	•	
	Holothuroidea	Dendrochirotida	*Echinopsolus acanthocola*	•	•	
			Indet holothurian (orange)	•		
			Ekmocucumis steineni	•	•	
	Ophiuroidea	Ophiurida	*Ophionotus victoriae*	•	•	
			Ophiurolepis sp.	•		
	Crinoidea		*Promachocrinus kerguelensis*	•		
Chordata	Ascidacea	Phlebobranchia	*Cnemidocarpa verrucosa*	•	•	
			Molgula enodis	•	•	
			Styella wandely	•	•	
			Pyura discoveryi	•		
			Pyura setosa	•		
			Ciona sp.?		•	
Chelicerata	Pycnogona	Pycnogonida	Pycnogonids	•	•	
Rhodophyta	Florideophyceae		Coralline alga 1.	•	•	
			Coralline alga 2.	•	•	
			Kallymenia antarctica	•	•	
			Hildenbrandia sp.	•	•	
	Phaeophyceae		*Desmarestia antarctica*	•	•	
			indet encrusting alga (brown)	•	•	

Species	
Aimulosia antarctica	•
Arachnopusia inchoata	•
Beania costata	•
Celleporella antarctica	•
Celleporella bougainvillei	•
Chaperiopsis protecta	•
Ellisina antarctica	•
Escaroides tridens	•
Fenestrulina exigua	•
Fenestrulina rugula	•
Figularia discors	•
Filaguria spatulata	•
Hippadanella inerma	•
Lageneschara lyrulata	•
Micropora brevissima	•
Micropora notialis	•
Microporella stenoporta	•
Smittina rogickae	•
Toretocheilum absidatum	•
Valdemunitella lata	•

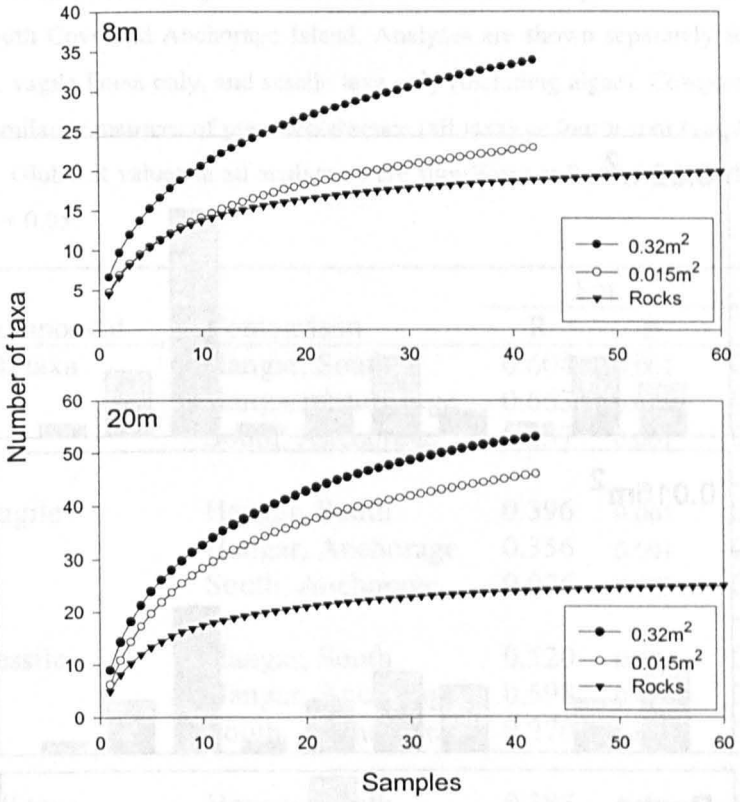


Figure 3.1 Taxon accumulation curves by depth (8 m and 20 m), and survey method (0.32 m^2 photoquadrats, 0.015 m^2 photoquadrats, and Rocks).

Table 3.2 One-way ANOSIM comparisons between benthic assemblages at 8 m and 20 m depths, by three methods of survey. Analyses are shown for: all taxa combined (including algae); vagile fauna only, and sessile taxa only (including algae). Comparisons were performed on Bray-Curtis similarity matrices of presence/absence (all taxa) or fourth root (vagile and sessile groups) transformed data.

Survey	Component	R	P
0.32m²	All taxa	0.512	0.001
	Vagile	0.390	0.001
	Sessile	0.506	0.001
0.015m²	All taxa	0.424	0.001
	Vagile	0.275	0.001
	Sessile	0.482	0.001
Rocks	Sessile	0.227	0.001

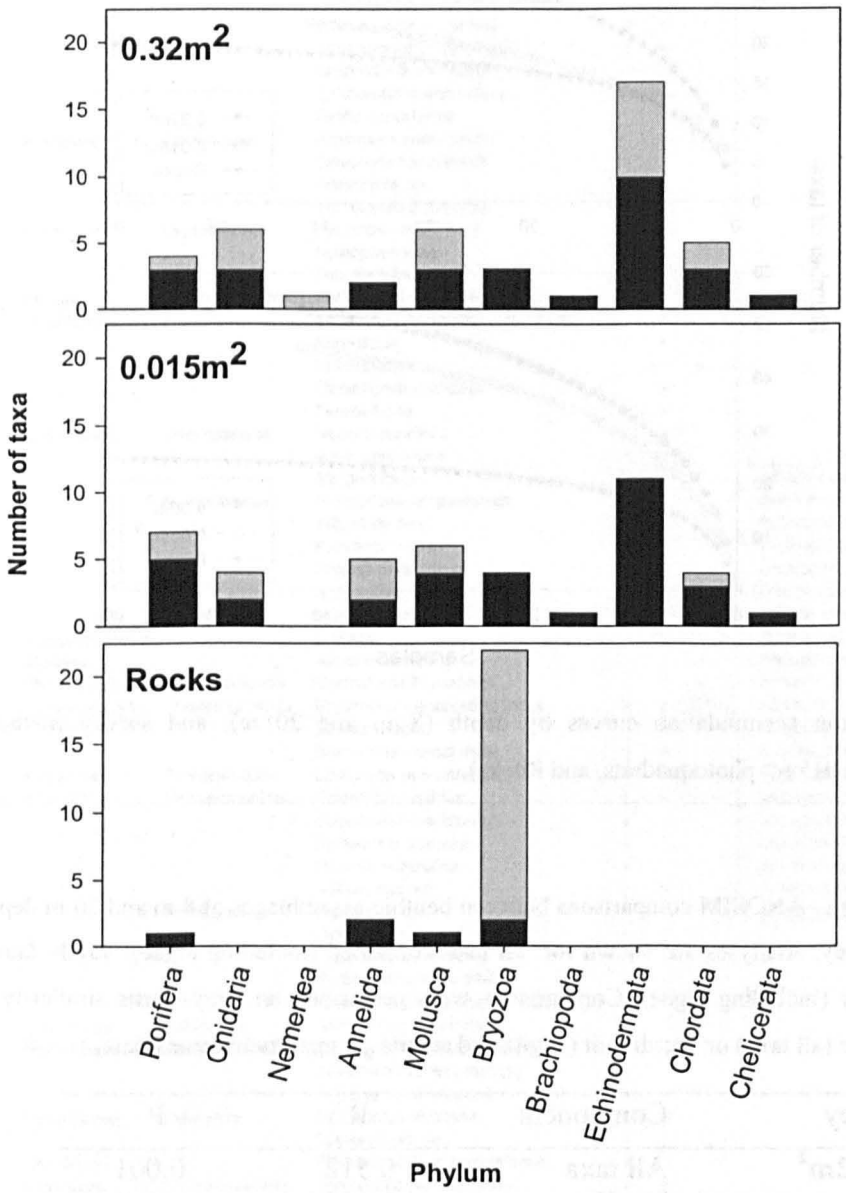


Figure 3.2 Numbers of taxa per phylum identified at each photographic scale (0.32 m^2 and 0.015 m^2 photoquadrats) and on collected rocks. Grey portions of bars in each graph show the number of species recorded only by that sampling method.

Table 3.3 Pairwise ANOSIM comparisons, at three scales of survey, between benthic assemblages at Hangar Cove, South Cove and Anchorage Island. Analyses are shown separately for: all taxa combined (including algae); vagile fauna only, and sessile taxa only (including algae). Comparisons were performed on Bray-Curtis similarity matrices of presence/absence (all taxa) or fourth root (vagile and sessile groups) transformed data. Global R values in all analyses were significant at $P < 0.01$. ns indicates non-significant comparisons at $\alpha = 0.05$.

			8m		20m	
Scale	Component	Comparison	R	p	R	p
0.32 m²	All taxa	Hangar, South	0.604	0.001	0.932	0.001
		Hangar, Anchorage	0.663	0.001	0.938	0.001
		South, Anchorage	0.257	0.001	0.257	0.001
	Vagile	Hangar, South	0.396	0.001	0.656	0.001
		Hangar, Anchorage	0.356	0.001	0.742	0.001
		South, Anchorage	0.076	0.079 ns	0.235	0.003
	Sessile	Hangar, South	0.520	0.001	0.766	0.001
		Hangar, Anchorage	0.598	0.001	0.854	0.001
		South, Anchorage	0.270	0.002	0.018	0.050 ns
0.015 m²	All taxa	Hangar, South	0.385	0.001	0.695	0.001
		Hangar, Anchorage	0.510	0.001	0.849	0.001
		South, Anchorage	0.218	0.002	0.097	0.030
	Vagile	Hangar, South	0.053	0.119 ns	0.227	0.046
		Hangar, Anchorage	0.309	0.003	0.145	0.040
		South, Anchorage	0.057	0.090 ns	0.048	0.136 ns
	Sessile	Hangar, South	0.747	0.001	0.718	0.001
		Hangar, Anchorage	0.530	0.001	0.835	0.001
		South, Anchorage	0.262	0.001	0.075	0.086 ns
Rocks	Sessile	Hangar, South	0.198	0.001	0.458	0.001
		Hangar, Anchorage	0.177	0.001	0.501	0.001
		South, Anchorage	0.013	0.263 ns	0.066	0.061 ns

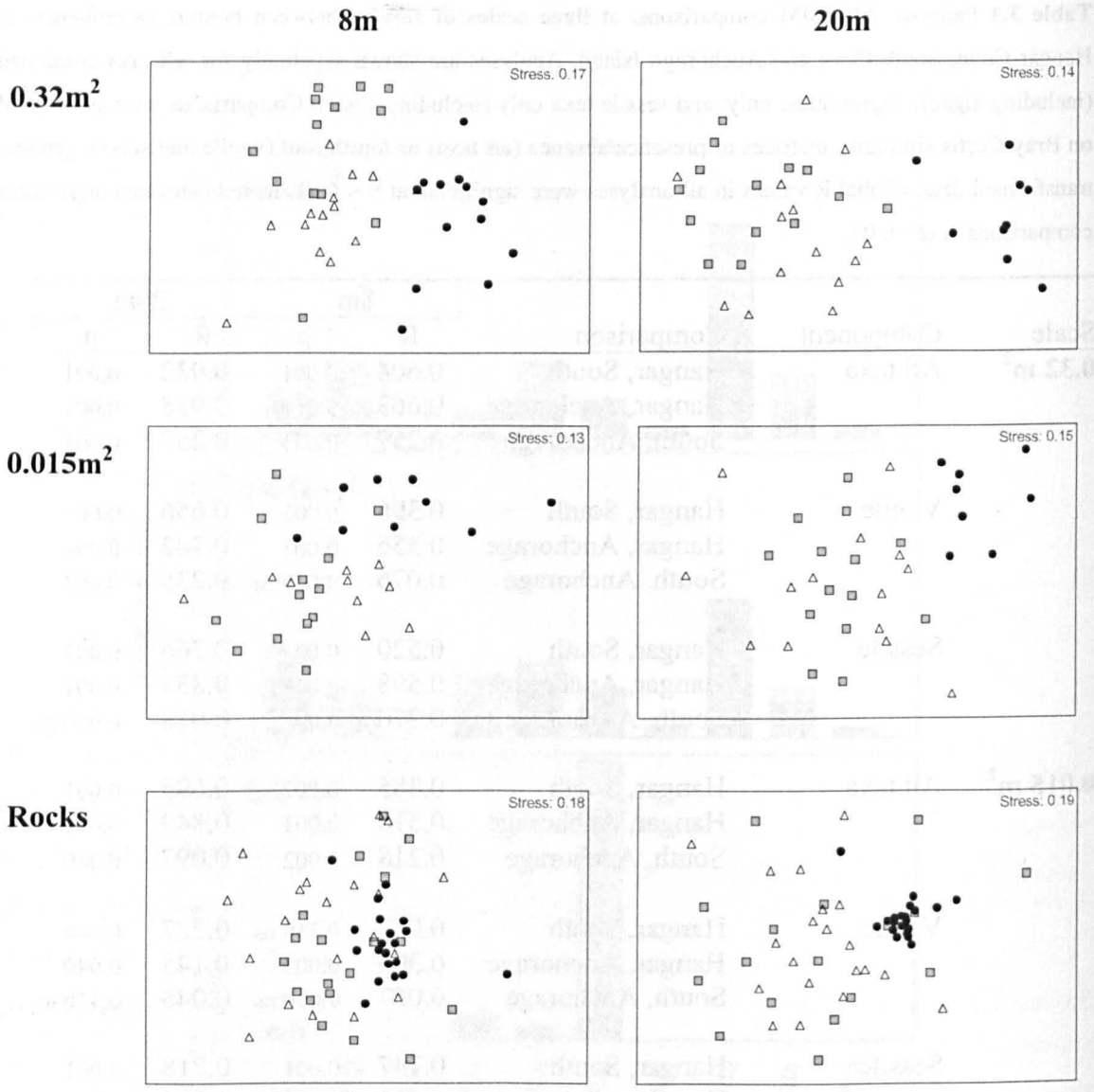


Figure 3.3 MDS ordinations of full data (fauna and algae) by survey method, depth, and location (△, South Cove, ▢ Anchorage Island, ● Hangar Cove). Bray-Curtis similarities are calculated from presence-absence data (0.32 m^2 and 0.015 m^2 photoquadrats), or fourth-root transformed data (Rocks). Note, the number of samples plotted may be less than 14 (0.32 m^2 and 0.015 m^2 scales) or 20 (rocks) as similarities are not calculated for samples in which no taxa were recorded (Clarke and Warwick 2001), and in some instances plots of very similar samples overlie each other.

Assemblage comparisons between depths (photographic surveys)

Vagile fauna

Vagile assemblages at both depths were dominated numerically by the limpet *Nacella concinna* and the regular echinoid *Sterechinus neumayeri*. At 8 m, all vagile assemblages were characterised by high densities of these two species (Figure 3.4, Figure 3.5), the cushion star *Odontaster validus* being the only other vagile species found consistently at this depth. *N. concinna* contributed most to the observed dissimilarity between depth groups at both scales of survey, mean abundance at 8 m being consistently around six times greater than at 20 m (Table 3.4). Mean densities of *S. neumayeri*, when averaged across all locations, showed no significant variation with depth (ANOVA on $\log(x+1)$ transformed data, $P > 0.05$). At the 0.015 m^2 scale, however, abundance estimates varied widely across locations, with mean densities at 8m ranging from 14.3 ± 10.3 $inds.m^{-2}$ at Hangar Cove to 290.5 ± 76.4 $inds.m^{-2}$ at Anchorage.

Assemblages at 20 m were characterized by a wider range of vagile species. Apart from *N. concinna*, the two survey scales identified different sets of species differentiating 20 m assemblages from those at 8 m. At the larger scale, the echinoderms *Ekmocucumis steineni, Echinopsolus acanthocola, Ophionotus victoriae* and *Diplasterias brucei*, and the limpet *Iothia coppingeri* were most characteristic of 20 m assemblages, whereas at the smaller scale *S. neumayeri, I. coppingeri,* pycnogonids, the mollusc *Margarella* sp. and *E. acanthocola* were most characteristic (Table 3.4).

Echinodermata was the most speciose phylum at 20 m, with 17 species recorded in total. Within the Echinodermata, Asteroidea was the most species-rich class, with at least nine species being identified, but abundances were generally low. *O. validus* was the most abundant asteroid with mean densities of 2.2 ± 0.6 $inds.m^{-2}$ at the larger scale, and 9.5 ± 5.4 $inds.m^{-2}$ at the smaller scale. Most asteroid species, however, were represented by <5 specimens across the entire survey area. By far the most abundant echinoderm, and indeed the most abundant vagile species recorded in any phylum, was *S. neumayeri,* which occurred in all 20 m quadrats with a mean abundance of 97.8 ± 11.0 $inds.m^{-2}$ at the larger scale and 142.9 ± 32.5 $inds.m^{-2}$ at the smaller scale. At the larger scale, at 20 m, *S. neumayeri* again showed no significant variation in abundance with location (ANOVA $F = 1.76$, $P = 0.18$) but at the smaller scale, densities in Hangar Cove were significantly lower than elsewhere (ANOVA $F = 8.0$, $P < 0.01$). The holothurian *E. steineni* was the

second most abundant echinoderm overall. It was found primarily at 20 m sites where the mean population density across all locations was 11.5 ± 2.6 inds.m^{-2}, but ranged from 0 to 65 inds.m^{-2}. Although holothurians were quantified by counts of individuals, *E. steineni* and *E. acanthocola* together were observed to cover a considerable proportion of the substratum at 20 m depth at South Cove and Anchorage locations.

Table 3.4 Vagile taxa contributing most (75% cut-off) to the dissimilarity between benthic assemblages at 8 m and 20 m depths for two photographic survey scales: 0.32 m^2 quadrats and 0.015 m^2 quadrats (SIMPER on fourth-root transformed data).

0.32m^2				
	Average abundance (inds.m^{-2})		Dissim. / SD	Contribution (%)
Taxon	20m	8m		
Nacella concinna	13.24	84.0	1.46	19.01
Ekmocucumis steineni	11.46	3.94	1.16	13.33
Odontaster validus	2.23	4.91	1.05	10.27
Iothia coppingeri	5.58	1.64	0.80	9.82
Sterechinus neumayeri	97.84	116.82	1.26	8.47
Echinopsolus acanthocola	5.36	0.07	0.74	7.77
Ophionotus victoriae	3.13	0.82	0.59	5.48
Diplasterias brucei	0.89	0.45	0.63	4.69
0.015m^2				
Nacella concinna	30.11	166.67	1.26	27.13
Sterechinus neumayeri	193.55	158.33	1.16	22.74
Iothia coppingeri	23.66	13.33	0.58	8.50
Pycnogonids	19.35	5.00	0.55	7.15
Margarella sp.	15.05	10.0	0.52	6.61
Echinopsolus acanthocola	27.96	3.33	0.50	5.35

Sessile taxa

Sessile assemblages at 8 m, at both scales of photographic survey, consisted predominantly of encrusting algal species. These covered 26.3 ± 3.1% of the substratum across all locations and contributed greatly to the total dissimilarity between assemblages at 8 m and 20 m (Table 3.5). A range of other sessile taxa were present at this depth, including cnidarians, polychaetes, sponges, bryozoans and macroalgae, but distributions were sporadic and mean coverage was generally very low (<2 %). The two scales of survey identified very similar sets of taxa as being characteristic of assemblages at this depth and only a greater abundance of serpulid polychaetes at 8 m detected by the 0.32 m^2 survey differentiated between the two scales (Table 3.5). This result, however, was due entirely to high densities of serpulids in Hangar Cove quadrats.

Sessile assemblages at 20 m were characterized at both scales by decreased coverage of encrusting algal species and increased coverage by a range of faunal species. At the larger scale, terebellid polychaetes showed the greatest areal coverage followed in decreasing order of coverage by the solitary ascidian *Cnemidocarpa verrucosa,* the cnidarian *Alcyonium antarcticum,* and an unidentified white demosponge. At the smaller scale these four taxa were again prominent but scale-related differences were apparent in the inclusion of spirorbid polychaetes and the greater prominence of encrusting bryozoans. Spirorbids were not quantifiable at the larger photographic scale but when measured at the smaller scale represented the greatest coverage of any faunal taxon at 20 m depth (Table 3.5). Minor taxa in terms of areal coverage but which were strongly associated with 20 m samples included the brachiopod *Liothyrella uva antarctica*, sponges, and leptothecate hydroids.

Table 3.5 Sessile taxa contributing most (75% cut-off) to the dissimilarity between benthic assemblages at 8 m and 20 m depths for two photographic survey scales: 0.32 m^2 quadrats and 0.015 m^2 quadrats.

0.32m^2				
	Average abundance (%area)		Dissim. / SD	Contribution (%)
Taxon	20m	8m		
Coralline alga 1	7.01	12.93	0.77	17.64
Coralline alga 2	0.07	3.65	0.57	12.39
Terebellid polychaetes	3.79	2.12	0.83	12.39
Indet. encrusting alga (brown)	0.16	9.68	0.71	10.71
Cnemidocarpa verrucosa	2.74	0.25	0.9	7.39
Alcyonium antarcticum	1.14	0.77	0.66	5.84
Serpulid polychaetes	0.74	3.05	0.41	5.48
Sponge 2	0.20	0.04	0.63	3.06
Kallymenia antarctica	1.43	1.66	0.27	2.80
0.015m^2				
Indet. encrusting alga (brown)	2.00	23.76	0.99	16.10
Coralline alga 1	9.08	25.55	1.04	15.62
Spirorbid polychaetes	4.91	1.97	1.06	11.65
Terebellid polychaetes	4.28	1.21	0.82	8.20
Bryozoans (encrusting)	2.71	1.13	0.82	6.96
Kallymenia antarctica	5.29	0.00	0.45	5.10
Coralline alga 2	0.00	1.98	0.42	3.37
Cnemidocarpa verrucosa	3.10	0.23	0.43	3.18
Alcyonium antarcticum	1.14	0.77	0.47	3.07
Sponge 2	0.20	0.04	0.47	3.01

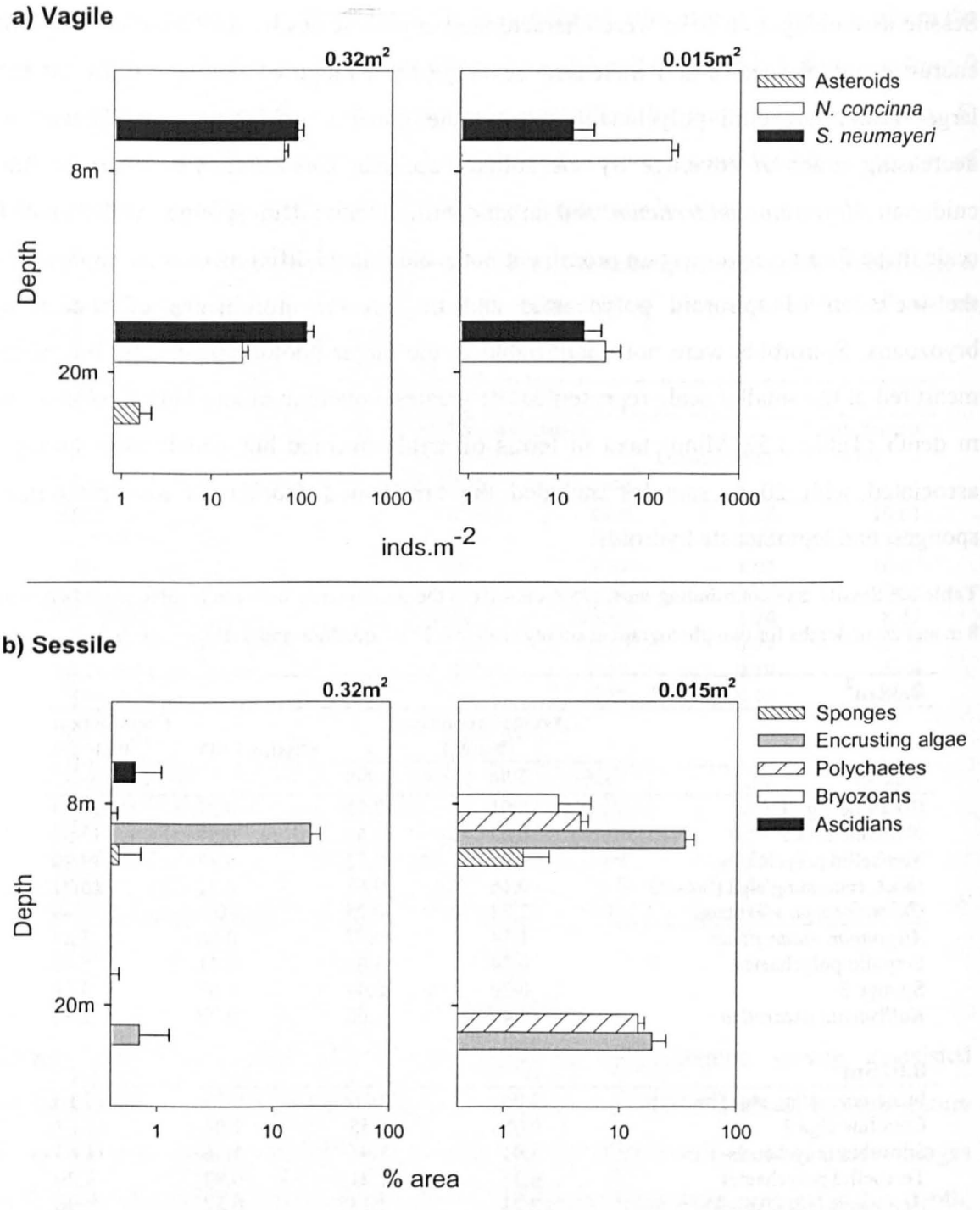


Figure 3.4 Benthic assemblages at Hangar Cove estimated at two scales of photographic survey (0.32m^2 quadrats and 0.015m^2 quadrats). Plots are means of selected vagile (a) and sessile (b) groups. Error bars show 1SE, n=14

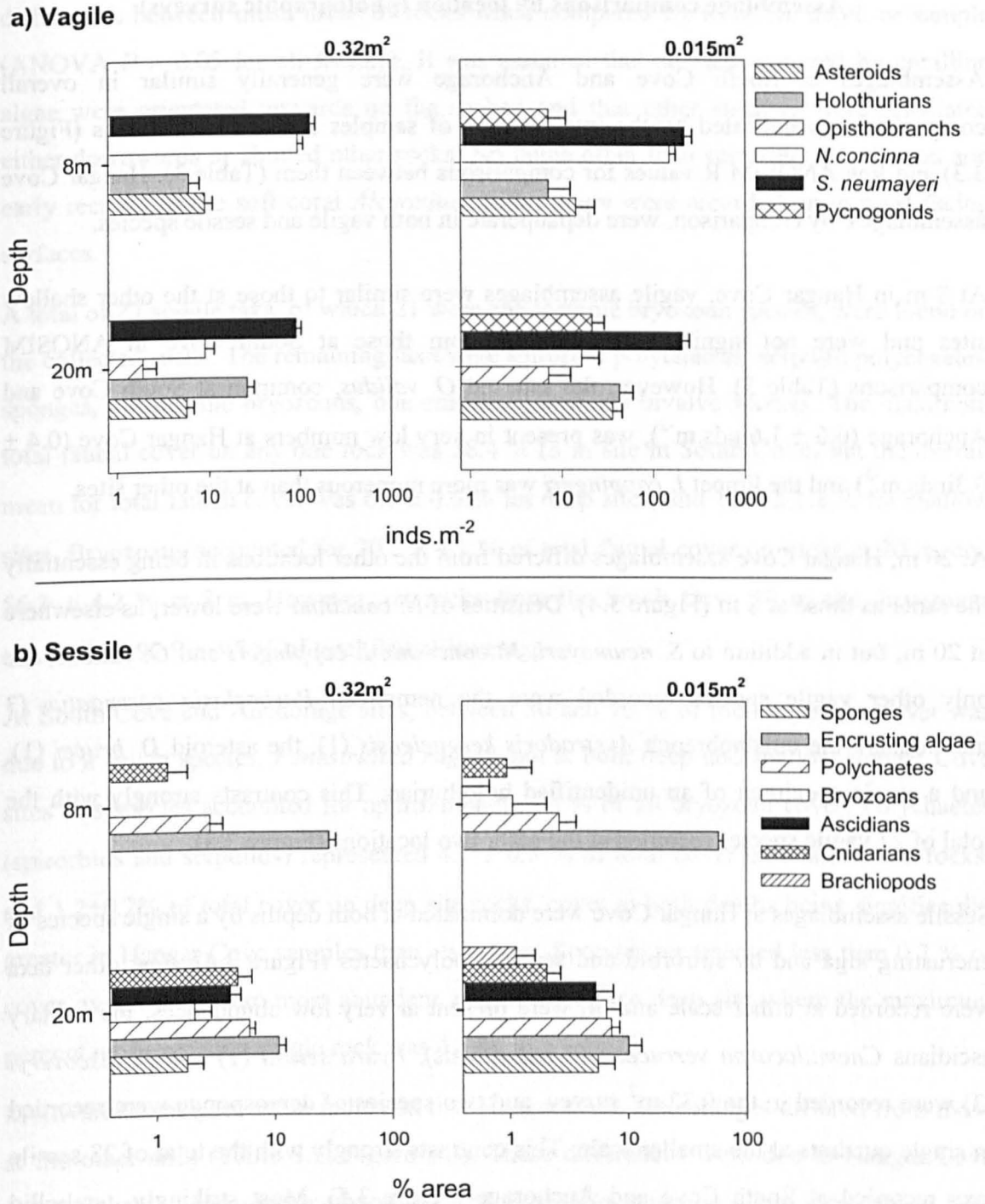


Figure 3.5 Benthic assemblages at South Cove and Anchorage Island estimated at two scales of photographic survey (0.32m^2 quadrats and 0.015m^2 quadrats). Plots are means of selected vagile (a) and sessile (b) groups averaged across both locations. Error bars show 1SE, n=28.

Assemblage comparisons by location (photographic surveys)

Assemblages at South Cove and Anchorage were generally similar in overall composition, as indicated by the interspersion of samples in MDS ordinations (Figure 3.3) and low ANOSIM R values for comparisons between them (Table 3). Hangar Cove assemblages, by comparison, were depauperate in both vagile and sessile species.

At 8 m in Hangar Cove, vagile assemblages were similar to those at the other shallow sites and were not significantly different from those at South Cove in ANOSIM comparisons (Table 3). However, the asteroid *O. validus,* common at South Cove and Anchorage (6.6 ± 1.6inds.m^{-2}), was present in very low numbers at Hangar Cove (0.4 ± 0.3inds.m^{-2}) and the limpet *I. coppingeri* was more numerous than at the other sites.

At 20 m, Hangar Cove assemblages differed from the other locations in being essentially the same as those at 8 m (Figure 3.4). Densities of *N. concinna* were lower, as elsewhere at 20 m, but in addition to *S. neumayeri, N. concinna, I. coppingeri* and *O. validus,* the only other vagile species recorded were the nemertean *Parborlasia corrugatus* (3 individuals), the opisthobranch *Austrodoris kerguelensis* (1), the asteroid *D. brucei* (1), and a single specimen of an unidentified holothurian. This contrasts strongly with the total of 27 vagile species recorded at the other two locations (Figure 3.5).

Sessile assemblages at Hangar Cove were dominated at both depths by a single species of encrusting alga and by spirorbid and serpulid polychaetes (Figure 3.4). Few other taxa were recorded at either scale and all were present at very low abundances: the solitary ascidians *Cnemidocarpa verrucosa* (6 individuals), *Pyura setosa* (1) and *P. discoveryi* (3) were recorded in the 0.32 m^2 survey, and two species of demosponge were recorded in single quadrats at the smaller scale. This contrasts strongly with the total of 28 sessile taxa recorded at South Cove and Anchorage (Figure 3.5). Most strikingly, terebellid polychaetes and the holothurian *Eckmocucumis steineni,* which were significant occupiers of space at both South Cove and Anchorage 20 m sites, were absent from Hangar Cove assemblages.

Rocks

The mean surface area of individual rocks was 374 cm^2 with a range from 106 cm^2 to 1084 cm^2. The total surface area surveyed was 4.48 m^2 and there were no significant

differences between mean areas of rocks when compared by location, depth or sample (ANOVA $P > 0.05$ for all factors). It was assumed that surfaces covered by coralline algae were orientated upwards on the seabed and that other surfaces were orientated either downwards or abutted other rocks. No fauna other than spirorbid polychaetes and early recruits of the soft coral *Alcyonium antarcticum* were recorded on upward facing surfaces.

A total of 27 sessile taxa, of which 21 were cheilostome bryozoan species, were found on the collected rocks. The remaining taxa were spirorbid polychaetes, serpulid polychaetes, sponges, cyclostome bryozoans, one cnidarian, and one bivalve species. The maximum total faunal cover on any one rock was 38.4 % (8 m site in South Cove) but the overall mean for total faunal cover was 6.5 ± 0.6 % for deep sites, and 12.5 ± 1.1 % for shallow sites. Bryozoans accounted for 70.2 ± 4.1 % of total faunal cover on rocks at 20 m, and 56.3 ± 4.2 % at 8 m. However, on rocks from the South Cove 20 m site, bryozoans contributed 92.9 ± 3.5 % of total faunal coverage.

At South Cove and Anchorage sites, between 30 and 70 % of total bryozoan cover was due to a single species, *Fenestrulina rugula,* but at both deep and shallow Hangar Cove sites this species accounted for approximately 90 % of all bryozoan cover. Polychaetes (spirorbids and serpulids) represented 4.1 ± 0.5 % of total cover on shallow site rocks, and 1.2±0.2% of total cover on deep site rocks, cover at both depths being significantly greater in Hangar Cove samples than elsewhere. Sponges represented less than 0.2 % of cover overall and were most abundant at the Anchorage deep site where the maximum percentage cover for a single rock was 4.8 %.

Multivariate analyses again indicated that Hangar Cove assemblages differed from those at the other sites (Table 3.3, Figure 3.3). These differences were due to Hangar Cove assemblages having greater abundances of *F. rugula*, spirorbids and serpulids at both depths, greater abundance of *Micropora notialis* at 8m, and consistently lower species richness than either Anchorage or South Cove.

DISCUSSION

Evaluation of photographic scale comparisons

Between the larger photographic scale (0.32m^2 photoquadrats) and the physical sampling element (rocks) of this survey, there are obvious resolution-related differences in the taxa recorded, and it is clear that each of these methods provides distinct and complementary data. Differences between results from the two scales of photographic survey, by contrast, are less clear. The spread of taxa across phyla is very similar for each of the two photographic scales (Figure 3.2) and as more taxa were recorded in the 0.32m^2 photoquadrats than at the smaller scale (for exactly the same sampling effort and image processing time) economies might be made by omitting the smaller scale. This would be a pragmatic option and either scale would evidently allow much the same ability to discriminate between depths and locations in multivariate analyses (Table 3, Figure 3.3). However, closer scrutiny of the lists of taxa recorded shows that, although similar, each scale emphasises a different size spectrum and different lifestyle modes. Thus, by omitting the smaller quadrats, the picture obtained would be biased towards larger, especially vagile, taxa and would lose resolution at smaller scales. Conversely, omission of the larger quadrats would under-represent larger, vagile and widely dispersed taxa while providing more detail on smaller sessile taxa.

For those taxa which are sampled at both photographic scales, further questions arise concerning which abundance estimate is the more accurate, and whether precision and repeatability (*sensu* Andrew & Mapstone 1987) are more important than absolute accuracy in facilitating comparisons with data from other studies. Variance is expected to increase (and hence precision to decrease) as sampling units are scaled up to standard units for comparison (Morin 1985). Thus, in the present study, lower precision would be anticipated from 0.015m^2 quadrats than from 0.32m^2 quadrats when each is scaled up to abundances per 1m^2. For vagile taxa, the precision (Pihl & Rosenberg 1982, Andrew & Mapstone 1987) of abundance estimates is, as predicted, clearly greater for the larger photographic quadrats (Figure 3.6a). For sessile taxa, by contrast, there is no clear or consistent difference between precision at the two scales (Figure 3.6b). Precision cannot, however, be used to infer accuracy, (Andrew & Mapstone 1987) and for many taxa in this survey estimates of abundance vary between scales. On the basis that what is not present is not counted, there is logic in assuming that the higher estimate in each case

will be the more accurate (Stretch 1985, Gray & Bell 1986). Although this logic is susceptible to distortion by outlier values (particularly when sample units are small in relation to the standard unit and replication is low), estimates for a majority of both vagile and sessile groups in the present study are higher at the $0.015m^2$ quadrat size (Figure 3.4, Figure 3.5) suggesting that they are more accurately sampled at this scale.

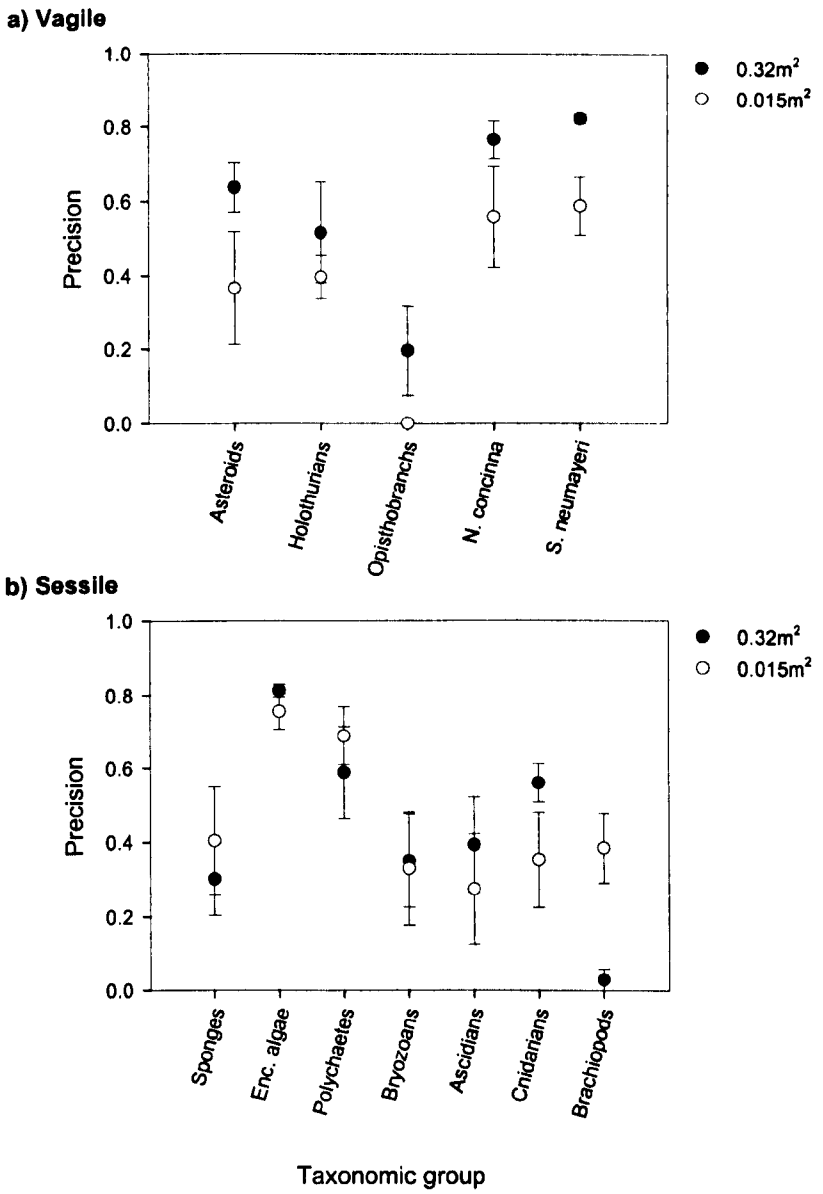


Figure 3.6 Comparisons of the precision of abundance estimates at two scales of photographic sampling ($0.32m^2$ and $0.015m^2$ quadrats) for a) vagile, and b) sessile taxa. Precision is calculated here as 1-(SE/mean), thus higher values indicate greater precision. Data are pooled across locations and depths, n=6, error bars show 1SE.

Absolute accuracy can only be achieved by exhaustive sampling, but for some taxa in South Cove comparisons can be made with data from an earlier study (Barnes & Brockington 2003) (Figure 3.7). These data were obtained from South Cove by collection of all fauna within two 0.25m^2 quadrats at each depth. They might, therefore, be expected to avoid the drawbacks of resolution and over-layering associated with photography but be subject to potential distortions associated with minimal replication and small total area covered. *N. concinna* and *S. neumayeri* abundance estimates from the 0.015m^2 photoquadrats are comparable to those from the excavated quadrats at both depths, suggesting that these abundance estimates are accurate. Estimates from the 0.32m^2 photoquadrats, by contrast are very similar to the other two surveys at 8m, but appreciably lower at 20m. Brockington et al. (2001) found that size distributions of *S. neumayeri* in South Cove were strongly skewed with depth: populations at 8m were predominantly of larger adults while those at 20m contained large numbers of small, immature individuals <10mm in diameter. This suggests that the difference in *S. neumayeri* estimates between photographic scales at 20m may be a resolution-related effect, with the 0.015m^2 quadrats detecting small individuals which are missed at the resolution of the larger quadrats. A similar pattern is evident for estimates of *N. concinna* abundances, suggesting that small individuals may again be missed at the resolution of the larger photographic quadrats. Interestingly, estimates of *E. steineni* abundance show a reversal of this effect which may be related to the larger body size and more clumped distribution (reflected in the greater variance of estimates) of this species in relation to quadrat size and total area sampled.

Ecological dominance of assemblages

A striking aspect of the assemblages surveyed here was the consistently high abundance of a few key taxa: the urchin *S. neumayeri,* the limpet *N. concinna,* the holothurian *E. steineni*, terebellid polychaetes and the solitary ascidian *C. verrucosa* in the photographic surveys, and the cheilostome bryozoan *F. rugula* at the scale of individual rocks. *S. neumayeri* has been reported from many sites around continental Antarctica and the Scotia Arc (e.g. Propp 1970, Bosch et al. 1987, Kirkwood & Burton 1988, Barnes & Brockington 2003, Cranmer et al. 2003) in numbers comparable to those recorded here and is believed to be ubiquitous in Antarctic nearshore waters (Arntz et al. 1994). The effects on benthic faunal and algal assemblages of grazing by urchins have been widely

documented in other latitudes (Ayling 1981, Chapman 1981, Elner & Vadas 1990, Andrew & Underwood 1993, Hunt & Scheibling 1997, Alves et al. 2001, Hill et al. 2003) and particular emphasis has been placed on the formation and maintenance of "urchin barrens" (Elner & Vadas 1990, Scheibling 1996) at high population densities. However, important effects on algal and molluscan populations have also been demonstrated at lower densities (Andrew & Underwood 1993).

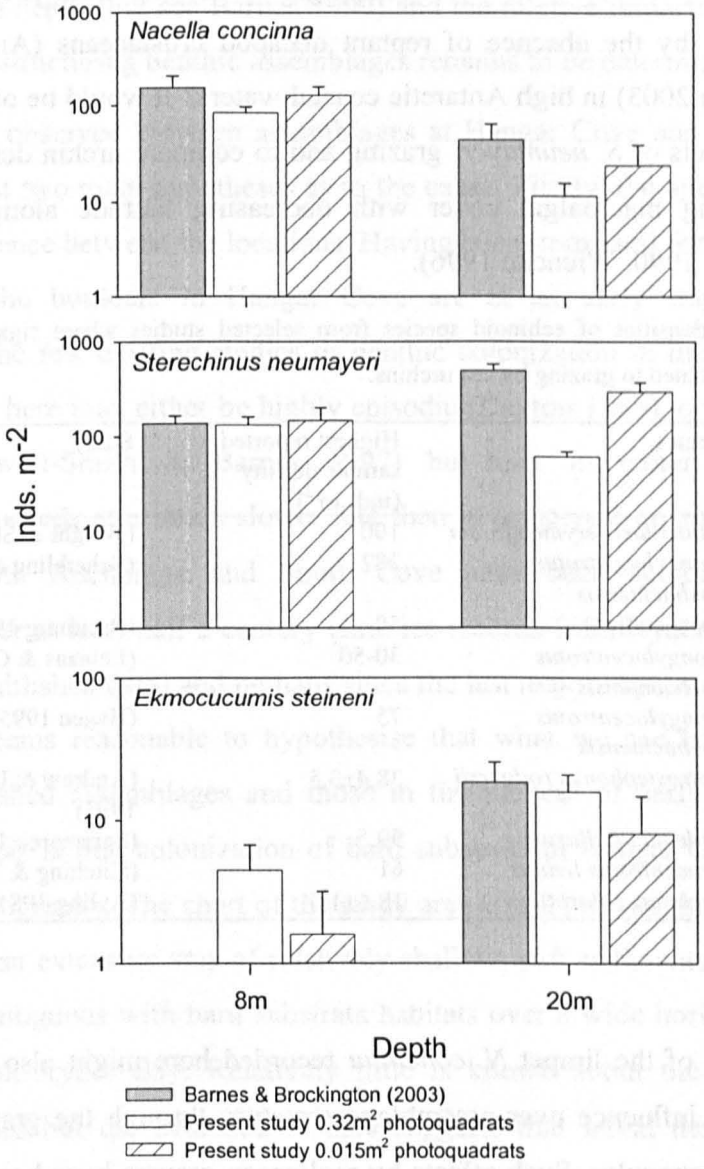


Figure 3.7 Comparison of abundance estimates for *N. Concinna*, S. *neumayeri* and *E. steineni* at two depths in South Cove. Barnes & Brockington 2003 data are from fauna collected in n=2 x 0.25m^2 quadrats at each depth, present study data n=14 photoquadrats. Values are means, error bars 1SE.

The densities of *S. neumayeri* recorded here are high by comparison with figures in the literature (Table 3.6) and it thus seems likely that *S. neumayeri* grazing may play a

significant role in structuring nearshore benthic assemblages in Antarctica. There are apparently no published studies on the influence of *S. neumayeri* grazing (but see Amsler et al. 1999) but it is interesting to speculate on the mechanisms involved in maintaining the patterns observed. That is, are observed patterns in the Antarctic shallow sublittoral maintained by grazing pressure from the consistently high densities of *S. neumayeri*, or are urchin populations here effectively released from space constraints (Dayton 1985, Leinaas & Christie 1996) by the low macroalgal cover, and from predation pressures (Scheibling 1996) by the absence of reptant decapod crustaceans (Arntz et al. 1994, Clarke & Johnston 2003) in high Antarctic coastal waters? It would be of interest both to determine the effects of *S. neumayeri* grazing and to compare urchin densities along the cline of increasing macroalgal cover with decreasing latitude along the Antarctic Peninsula (Dayton 1990, Wiencke 1996).

Table 3.6 Reported densities of echinoid species from selected studies where significant assemblage effects have been attributed to grazing by sea urchins.

Region	Species	Highest reported sample density (inds.m^{-2})	Study
SE Australia	*Heliocidaris erythrograma*	100	(Wright & Steinberg 2001)
Nova Scotia	*Strongylocentrotus droebachiensis*	382	(Scheibling et al. 1999)
California	(not specified)	50	(Breitburg 1996)
Norway	*Strongylocentrotus droebachiensis*	30-50	(Leinaas & Christie 1996)
Norway	*Strongylocentrotus droebachiensis*	75	(Hagen 1995)
NSW Australia	*Centrostephanus rodgersii*	38.4±3.5	(Andrew & Underwood 1993)
Jamaica	*Diadema antillarum*	99.5	(Sammarco 1982)
Ireland	*Paracentrotus lividus*	61	(Kitching & Thain 1982)
New Zealand	*Evechinus chloroticus*	18.6±1.6	(Ayling 1981)

The high densities of the limpet *N. concinna* recorded here might also be expected to exert a significant influence over assemblage structure through the grazing of settling algal and faunal propagules. Such effects by molluscan grazers have been demonstrated in other latitudes (Hawkins & Hartnoll 1983, Lubchenco 1983, Turner & Todd 1991) but other than a correlation between *N. concinna* densities and reduced algal cover in the Antarctic intertidal (Kim 2001), there are no published studies on the wider influence of this species.

Observed patterns

The pronounced assemblage differences between depths observed in this survey are characteristic of Antarctic sublittoral habitats (Dayton 1990, Arntz et al. 1994, Barnes 1995b) and are believed to be caused principally by a gradient of decreasing frequency of disturbance by ice with depth (Dayton 1990, Arntz et al. 1994, Barnes 1999). To date, however, no studies have been published which quantify the variation in frequency of ice disturbance with depth (but see Barnes 1999) and the relative importance of abiotic and biotic factors in structuring benthic assemblages remains to be determined.

The differences observed between assemblages at Hangar Cove and those at the other locations suggest two main hypotheses as to the cause. Firstly, the age of the substratum is a major difference between the locations. Having been immersed for just one decade, it is likely that the boulders in Hangar Cove are at an early stage of assemblage development. The few existing studies of benthic colonization in the Antarctic suggest that recruitment here may either be highly episodic (Dayton 1989), or continuous at low intensity (Stanwell-Smith & Barnes 1997) but that in either case assemblage development proceeds at a much slower rate than in temperate or tropical latitudes. As substrata at both Anchorage and South Cove have been subject to colonization continuously over at least half a century (first ice records from Ryder Bay 1947, Alison Cook BAS unpublished data) and perhaps since the last major expansion of the Antarctic ice sheets, it seems reasonable to hypothesise that what we see here is a difference between established assemblages and those in the process of early colonization. The second hypothesis is that colonization of hard substrata in Hangar Cove is affected by local seabed topography. The chart of the study area (fig. 1) shows that the Hangar Cove location lies in an extensive area of relatively shallow, soft sediments whereas the other locations are contiguous with hard substrata habitats over a wide horizontal and vertical range throughout Ryder Bay. Relatively little is known about the larval ecology of Antarctic benthos but the evidence to date suggests that larval densities are low by comparison with other latitudes (Stanwell-Smith et al. 1999) and, for some groups at least, the paradigm of reduced incidence of pelagic larvae in high latitudes (Mileikovsky 1971) still appears to hold (Pearse et al. 1991b, Poulin & Feral 1996, Pearse & Lockhart 2004). Furthermore, in temperate and tropical latitudes many sessile groups tend to reproduce by means of short-dispersal, lecithotropic larvae (Jackson 1986). If dispersal

distances of these taxa are indeed limited, it may be that sites in Hangar Cove are isolated from established source populations. Consequently, recruitment may be limited to taxa, such as *S. neumayeri,* which have widely dispersing planktonic larvae (Bosch et al. 1987), and those, such as spirorbids and *F. rugula*, which are abundant in the immediate sublittoral (the only hard substratum habitat which is contiguous with the survey sites in Hangar Cove) and thus are able to colonize by a succession of shorter dispersal events.

Conclusions

Photographic techniques provide a practical, non-destructive method for surveying hard substratum benthic assemblages. Relatively small differences in the scale of observation, however, may emphasize different size spectra or types of biota and the choice of survey scale involves a trade-off between resolution and area covered. Sampling at a range of scales affords a means of overcoming these problems and the relative simplicity and speed with which photographic surveys can be undertaken allows greater scope for such multi-scale surveys than do conventional techniques. The subsequent analysis of images may be as time-consuming as the processing of conventional samples but photography has advantages in that samples can be analysed to whatever level is appropriate (or economic) for the immediate study yet can be re-evaluated at any subsequent time if greater detail is required.

At the scales examined, the assemblages described in this survey are notable for the numerical dominance of a few species. In light of findings from lower latitudes, the abundance of *S. neumayeri* and *N. concinna* in particular might be expected to exert significant influences in structuring assemblages. Work on these species to date has concentrated on physiology or autecology (e.g. Bosch et al. 1987, Brockington & Clarke 2001, Brockington et al. 2001, Fraser et al. 2002a) and broader investigations of their ecological roles would be of great interest. Differences identified between depths and between Hangar Cove and the other study locations highlight further areas where more detailed ecological research is required for the understanding of structuring processes in the Antarctic benthos. Most obviously, the paradigm that depth zonation is caused by ice disturbance remains to be quantitatively demonstrated. There is also, however, a need for data both on realised dispersal distances and on rates of assemblage development as these factors will inevitably interact with ice disturbance gradients in determining observed patterns of distribution.

Chapter 4 – Overview of recruitment studies

Chapter 4 – Overview of recruitment studies

INTRODUCTION

The main recruitment study in the following chapters incorporates two parallel experiments:

1) a study of seasonal short-term recruitment patterns using artificial substrata retrieved and replaced at monthly intervals,

2) a study of the development of sessile assemblages over a 3 yr period using continuously immersed artificial substrata.

These studies share the same spatial design and equipment. This chapter, therefore, describes the equipment and layout used and presents a rationale and critique of the experimental design.

The principal objectives of the short-term recruitment study were to evaluate temporal and spatial variability in the abundance and taxonomic diversity of sessile organisms settling to the seabed. The term 'short-term recruitment' is used here in preference to settlement because, in this context, settlement is defined as the total number of competent larvae arriving at the substratum (Keough & Downes 1982, Connell 1985) and in a study such as this there is likely to be mortality of settling larvae in the interval between deployment and retrieval of substrata. The objectives of the continuous-immersion study were to measure seasonal and annual rates of growth and mortality of sessile taxa. The spatial design was intended to enable measurement of variability between study locations, between depths, and between upward-facing ('upper') and downward-facing ('lower') substratum surfaces.

MATERIALS & METHODS

Design of settlement plate units

General considerations

Among the few benthic colonisation studies which have been undertaken in Antarctica (Brand 1980, Dayton 1989, Rauschert 1991, Barnes et al. 1996, Stanwell-Smith & Barnes 1997), there is a consensus that rates of recruitment are generally low and that loss of experimental substrata through ice-related disturbance is common. These two

factors, therefore, were the principal considerations in designing the equipment and strategy for the present study.

The anticipated low levels of recruitment suggested the need to sample a large total area and to incorporate adequate replication at all scales of investigation. To this end, individual settlement plates were designed to be larger than in many previous studies, and both the number of experimental sites and the number of replicate plates within each site were made as large as practicable. The expectation of ice damage, however, suggested the need for small independent units rather than the larger racks holding several plates which have often been used in recruitment studies (e.g. Todd & Turner 1986, Stanwell-Smith & Barnes 1997).

From a pragmatic point of view, smaller independent units can be positioned in protected niches, thus affording some protection from ice, and are more easily, quickly, and affordably replaced should damage occur. In terms of experimental design, they have the further advantage of being true replicates and that localised ice damage is unlikely to remove all units within a site. Thus, as individual units are easily replaceable, ice damage can be expected only to reduce replication temporarily, rather than destroying all plates within the affected site. Further requirements were that the settlement surfaces should be suitable for photographic monitoring *in situ*, that both upper and lower plate surfaces should be accessible for routine monitoring, and that it should be possible to monitor both short-term recruitment and long-term assemblage development on the same experimental unit.

Construction details

Plates were constructed from opaque, black, acrylic sheet. This material has been used successfully in recruitment studies in other parts of the world (Turner & Todd 1993, Todd & Keough 1994, Todd 2003). It is inexpensive, simple to machine, easily transported, uniform throughout, and provides excellent visual contrast for identifying recruits. As 35 mm cameras were to be used for monitoring of continuously immersed plates, a rectangular plate design matched to the aspect ratio of the film frame was used. This made more efficient use of the resolving power of the imaging system than square plates and allowed 50 % greater area to be sampled per image.

The maximum size of the plate was dictated by the characteristics of the lens used and the level of resolution required. Tests showed appreciable pincushion distortion at the

frame edges when using either of the available lenses (35 mm and 28 mm uw Nikkor), which made area measurements unreliable. For this reason, the overall size of the plates was designed to fill the image frame when using the wider-angle lens (28 mm) but only a central, relatively distortion-free analysis area was to be measured. The resulting plates were 250 mm x 150 mm x 5 mm with a central analysis area of 150 mm x 100 mm.

The corners of the analysis area and the plate centre were marked by 1.5 mm diameter holes drilled through the plate and refilled with white silicon mastic (Figure 4.1). These points were used to define the analysis area in photographs of the plates and to calibrate measurements during image analysis. This method of delineation avoided surface irregularities associated with engraved lines, which can influence settlement behaviour (Pech et al. 2002, Todd 2003), or the use of inks (Stanwell-Smith & Barnes 1997) which may fade with repeated use. All plates were made on site at Rothera using a purpose-built jig to ensure consistency of measurements and alignment.

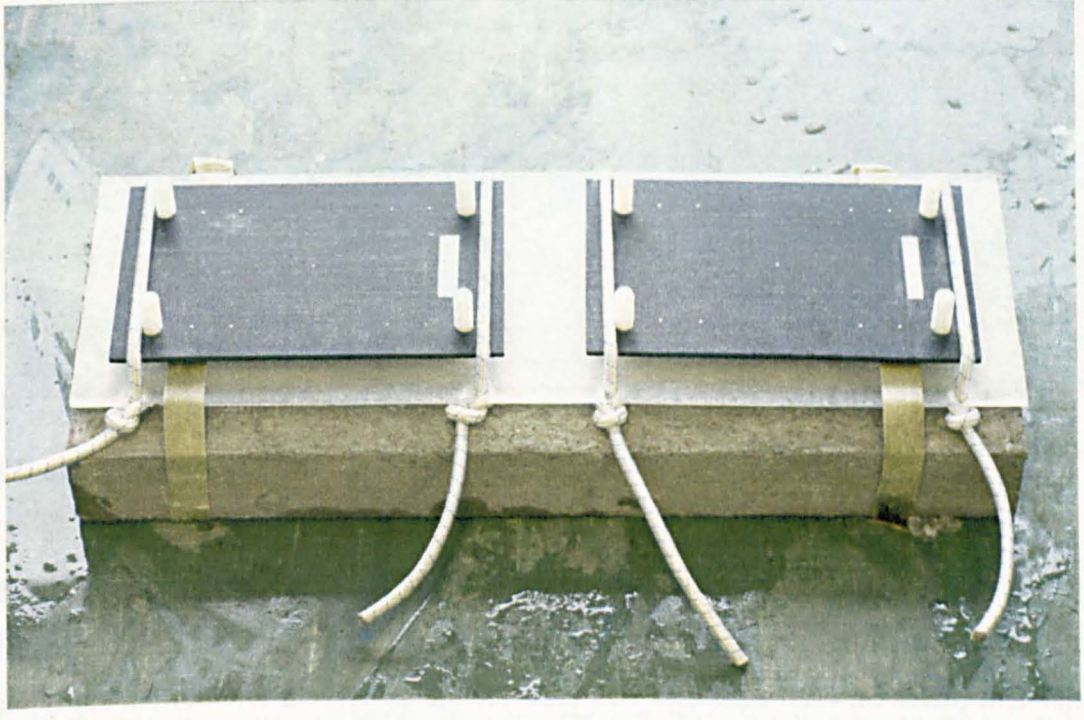


Figure 4.1 Settlement plate unit design. The left hand plate on each unit was replaced at monthly intervals to monitor short-term recruitment. The right-hand plate remained *in situ* throughout the study and was monitored photographically to follow assemblage development over the 3 years of the study.

The requirement to be able to monitor both upper and lower plate surfaces *in situ* (for the continuous immersion study) prevented use of a conventional bolted attachment, as this would have been too time-consuming within the constraints of cold-water dive regimes and problematic wearing thick gloves. Instead, individual plates were located on four upright M12 nylon studs protruding from an acrylic base panel. The studs were retained in place in the base panel by nylon nuts which served as spacers to maintain a 10mm gap between the lower analysis surface of the settlement plate and the base panel. Gap size has been shown to influence recruitment of sessile invertebrates (Todd & Turner 1986) and the gap size of 10 mm was chosen here as the median gap size tested by Todd & Turner (1986). Settlement plates were secured by two elastic strops which fasten by engaging a terminal knot in slots cut in the base panel.

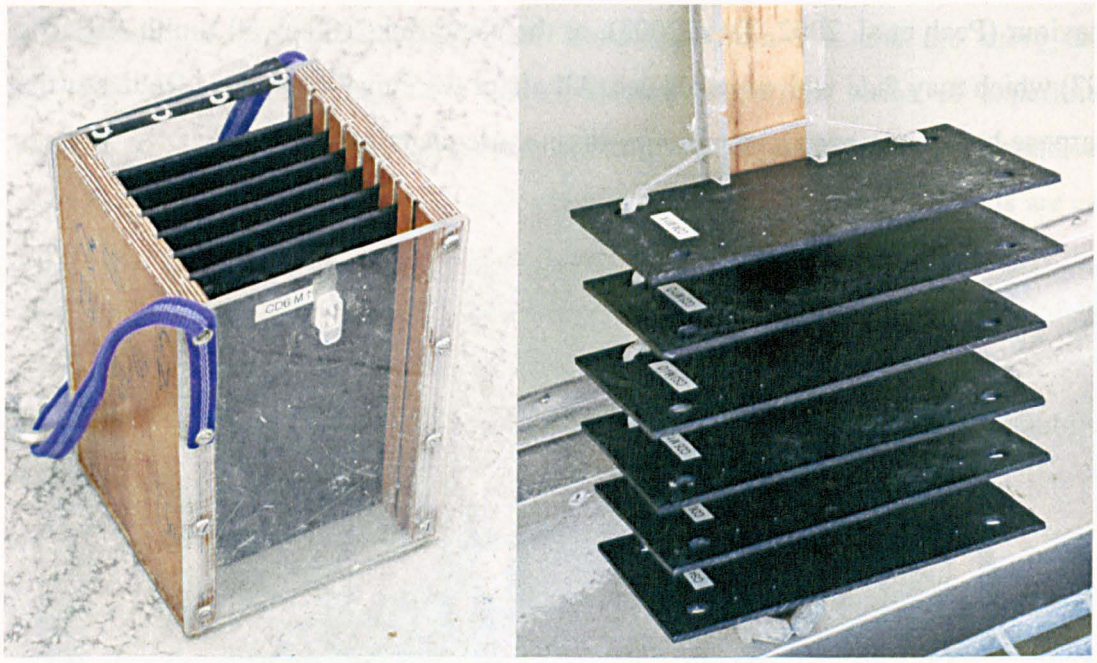


Figure 4.2 Settlement plate transport box (left) and aquarium storage rack (right).

Each base panel held two settlement plates side by side and was, in turn, rigidly attached by webbing straps to a 25 kg concrete sinker (Figure 4.1). Of the two settlement plates on each unit, one was used for the short-term recruitment study and was replaced at approximately 30-day intervals ("Monthly" plates). The other plate remained *in situ* throughout the study and was monitored photographically to follow assemblage development over an extended period ("Continuous" plates). All deployments, retrievals, and *in situ* photographic monitoring were performed by divers

using SCUBA and at all times plates were transported in purpose-built, water-tight boxes to ensure that analysis surfaces were neither touched nor exposed to air. While pending examination, plates were suspended on purpose-built racks in tanks supplied with 100 μm filtered seawater at ambient temperature (Figure 4.2).

Experimental design

Arrays of six settlement plate units were deployed at two depth sites (8 m and 20 m) at each of the three locations (Hangar Cove, South Cove, and Anchorage Island – see Chapter 2) resulting in a total of 36 units. The study is thus stratified by depth, locations encompass local variability on the scale of ~5 km, and individual units are replicated (n = 6) within each depth × location site. Individual units within each array were placed either on, or immediately adjacent to, hard substrata, were approximately horizontal in orientation, and were positioned on ledges or against boulders in such a way as to minimise risk of dislodgement by ice. At 2 0m, the resulting arrays were essentially linear along the nominal isobath, spanned 6 to 8 m horizontally, had distances between adjacent units of 0.3 m to 1.0 m, and varied in depth by less than 1 m. At 8 m, constraints of seabed topography resulted in more haphazard arrangements of units and at all locations actual depths ranged between 7 m and 9 m.

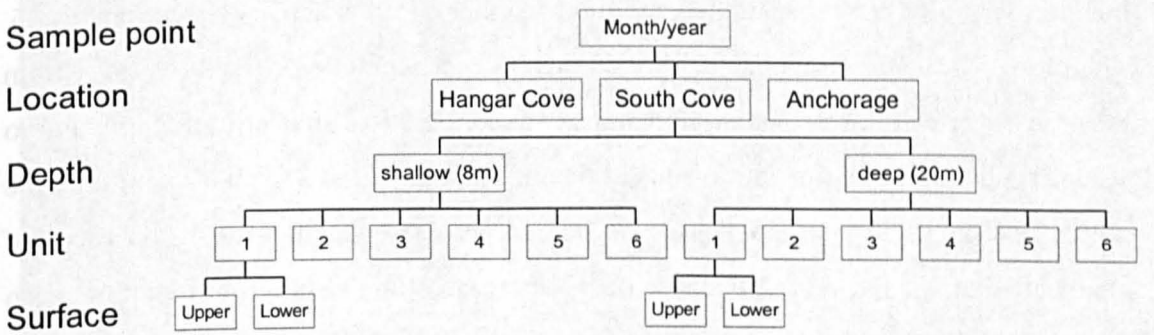


Figure 4.3 Experimental design for recruitment studies. At each of the 3 locations, there is a shallow site at 8 m depth and a deep site at 20 m depth (for clarity, only South Cove is shown in detail). Within each site there are 6 replicate settlement plate units, and each individual plate has an upward- and a downward-facing analysis surface. The short-term recruitment (monthly replacement plates), and long-term recruitment (continuous immersion plates) studies share the same layout: each replicate unit holds one plate for each study.

Rationale for the design

The principal shortcoming of this experimental design is the lack of replication of sites at each depth within each location (Figure 4.3). The consequence of this is that there is no logical test for any effects arising from interactions between locations and depths (see Underwood 1997, Bowden et al. 2001). Thus, the design involves the implicit assumption that any effect of depth on benthic assemblages will be consistent across the study area. This limitation was understood at the planning stage and the decision to adopt the 3-location design without replication of depth sites was based on a trade-off between scientific aims and logistic constraints.

It was considered to be important that the results should give some idea of variability across the local area. Therefore, it was planned to study a minimum of 3 locations. However, the expectation of damage to equipment from ice impacts required that there should also be redundancy within the design, which could potentially be achieved by increasing replication at any level of the design, from locations to individual settlement units. The maximum total number of dives which could be allocated to the study (larvae and recruitment aspects combined) per month was 6, thus precluding the option of increasing the number of locations. Initial trials showed that the maximum number of replicate settlement plate units which could be sampled at each depth at each location was also 6, which limited the total number of units across 3 locations to 36. Therefore, the only practicable way to achieve replication of depth sites within locations, while retaining 3 study locations, was to include 2 sites at each depth and to reduce replication of units within sites to the minimum level of 3. This was initially the preferred design, as units could still be pooled across replicate sites in the event of major ice damage. However, because of the increased time required to move between sites at each depth, this layout proved impractical within diving constraints. Therefore, the unreplicated design described above was adopted.

Caging

Initial reconnaissance of the study area showed high abundances of vagile grazers, particularly the urchin *Sterechinus neumayeri* and the limpet *Nacella concinna* (Chapter 3). Grazing by similar taxa in temperate latitudes can be a dominant factor controlling the recruitment of sessile fauna and algae (Reviewed by Gosselin & Qian

1997, Hunt & Scheibling 1997). Therefore, a caging treatment was incorporated in the experiment to evaluate the effects of such grazing.

Cages were constructed from plastic garden mesh (10 mm square-aperture) held together with nylon cable ties and with an opening upper section secured by shock-cord loops to allow access for plate exchanges and monitoring. Each cage enclosed one complete settlement plate unit and at each study site three plate units (i.e. half of all units) were caged. Caged treatments were interspersed with open units. To control for potential cage effects, such as increased sedimentation, shading, or flow modification, 3 partially caged control units were installed at each depth in South Cove only (Figure 4.4). These were identical to the caged settlement plate units except that two sides of the cage were removed, allowing access to the settlement plates by grazers. Controls were not installed at the other locations because of limitations of dive time and site accessibility. This experimental design, therefore, includes the implicit assumption that there is no interaction between cage effect and location.

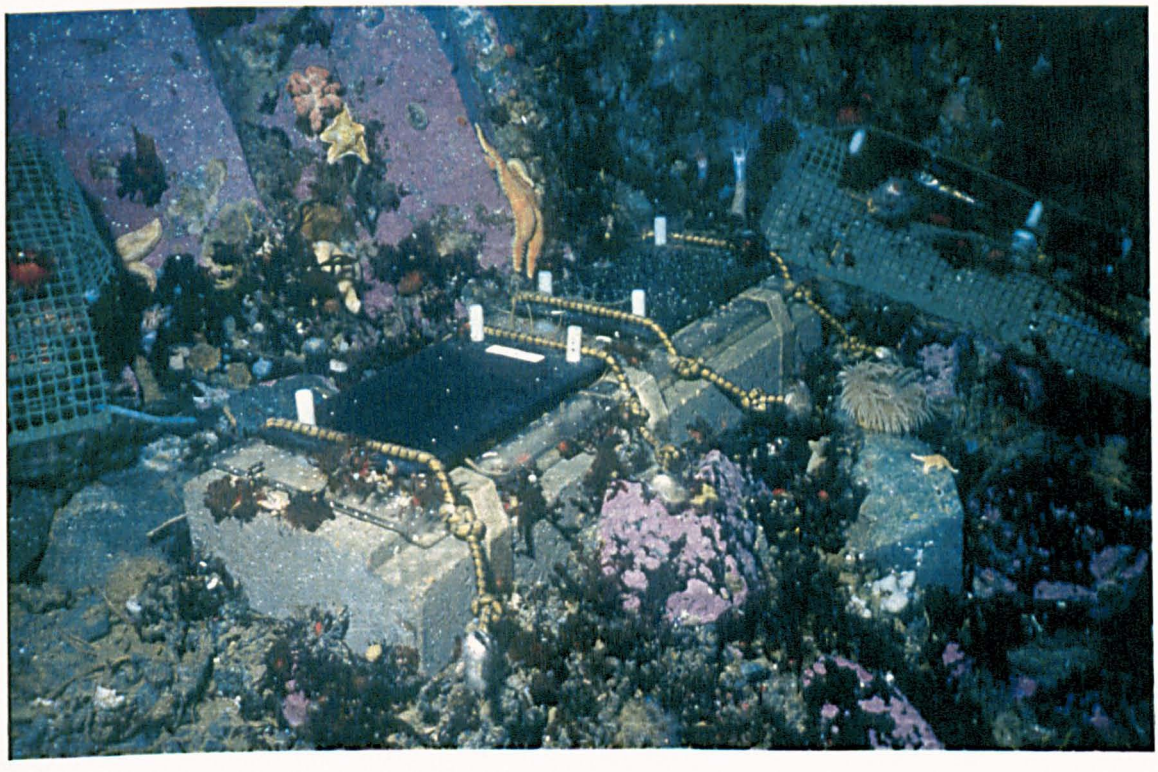


Figure 4.4 Settlement plate units at 20 m in South Cove. Uncaged (foreground), caged (far left), and cage control (right) units are visible.

Within the first few months of deployment, however, it was clear that the cages were not effective at excluding vagile macrofauna. The cage design was prone to distortion,

allowing gaps to form at panel joins, and the closure system proved awkward to operate, which occasionally resulted in cages being left partially open. These design failings allowed access to the plates by urchins, limpets and asteroids but other macrofauna, particularly adult holothurians, nemerteans, and terebellid polychaetes, were also able to enter directly through the cage mesh. For these reasons, the caging treatment was considered largely uninterpretable and a decision was made to treat all units, caged and open, at each site as replicates. Thus, differences between caged and uncaged plates were considered to represent the influence of environmental heterogeneity of the seabed.

Chapter 5 – Seasonality of recruitment

[The data in this chapter are also presented in: Bowden DA (2005) Seasonality of recruitment in Antarctic sessile marine benthos. Marine Ecology Progress Series **297:** 101-118]

Chapter 5 – Seasonality of recruitment

INTRODUCTION

Accurate data on the timing, abundance and diversity of recruitment are central to understanding the dynamics of benthic ecosystems (Connell 1985, Underwood & Fairweather 1989, Gaines & Bertness 1992, Caley et al. 1996, Connolly & Roughgarden 1999, Connolly et al. 2001, Gimenez 2004). Consequently, in temperate and tropical regions there has been considerable research on patterns of recruitment; much of this work concentrating on individual species or assemblages in the rocky intertidal (e.g. Connell 1985, Menge 1991, Gaines & Bertness 1993, Underwood & Anderson 1994, Booth & Brosnan 1995, Menge 2000). In higher latitudes, the deep sea, and in sublittoral environments in general, by contrast, there are few published studies of recruitment. For the validation of any general model of benthic community dynamics, however, there is a need for data from assemblages across a broad range of environments and Todd (1998) has stressed the requirement for investigation of whole assemblages, rather than single species, in assessing the relative importance of pre- and post-settlement processes.

In Antarctic nearshore waters, the combination of extremely low, relatively constant, seawater temperatures, a naturally occurring gradient of decreasing ice-mediated disturbance with depth, highly seasonal primary production, and biogeographic isolation over some 25 million years, has created an environment in which rates of growth, reproduction and colonization among native taxa are apparently very slow (Pearse et al. 1991b, Arntz et al. 1994, but see also Barnes & Arnold 2001b), yet disturbance is frequent. Despite this, nearshore marine benthic assemblages in the Antarctic are diverse and support high standing stocks (Brey & Clarke 1993, Arntz et al. 1994, Clarke & Johnston 2003). The region, therefore, presents opportunities for studying the life-history adaptations by which slow-growing benthic species are able to persist in habitats with highly seasonal food input and frequent natural disturbance. To date, however, very few studies of benthic recruitment have been conducted in the Antarctic and published data are sparse.

Dayton (1989) deployed extensive settlement panel arrays over a ten year period at McMurdo Sound (77° 50′ S, 166° 40′ E) but published no data from this study other

than an observation that, at one site, there was no colonization of panels after 5 yr but heavy colonization by a diverse assemblage after 10 yr. Also at McMurdo, Pearse & Pearse (1991) immersed small glass slides and published a brief, qualitative, report describing a sparse assemblage dominated by bryozoans at the end of 1 yr. At King George Island (62° 12′ S, 57° 54′ W) Rauschert (1991) reported heavy growth of ascidians on three panels recovered after three years immersion but the main part of this experiment was lost. In the most detailed study to date, Stanwell-Smith and Barnes (1997) at Signy Island in the South Sandwich Islands (60° 43′ S, 45° 36′ W), identified continuous low levels of recruitment at bi-monthly intervals throughout an annual cycle. The latter study (Stanwell-Smith & Barnes 1997) is the only one with quantitative seasonal information but the data are limited in both spatial and taxonomic resolution by comparison with many temperate and tropical studies and are from an arguably atypical location in the maritime Antarctic.

In this context, the principal objective of the present study was to generate high resolution data on the seasonality, diversity and abundance of early recruitment in hard-substratum sessile assemblages at a more characteristic Antarctic location. More specifically, characteristics of the environment and the distributions of assemblages on natural substrata suggested three hypotheses. Firstly, in light of the brief and highly seasonal phytoplankton bloom characteristic of these latitudes (Clarke & Leakey 1996), it was hypothesised that recruitment of the majority of sessile taxa would coincide with the period of maximum food availability during the summer months (Dec-Feb). Therefore, the project aimed to identify taxon-dependent differences in recruitment period. Secondly, nearshore benthic assemblages in the Antarctic are characterised by conspicuous zonation with depth which is thought to be largely attributable to the decreasing frequency of ice scour with increasing depth (Barnes 1999, Gutt 2001). Assemblages at depths shallower than ~10-15 m are generally less diverse and substrata are less heavily colonised than those at depths below ~15 m. It was, therefore, hypothesised that the taxonomic diversity of recruitment would be reduced at shallower depths. Thirdly, Stanwell-Smith and Barnes (1997) monitored recruitment only to the lower surfaces of settlement plates, having previously observed that the undersurfaces of rocks were colonized more extensively by sessile fauna than were upper surfaces. Observation of natural substrata in these regions, however,

indicates that many sessile taxa do persist and grow on exposed, upward facing surfaces (e.g. solitary ascidians, brachiopods, sponges, octocorals), indicating that these species, at least, must recruit to upper surfaces. By simultaneously monitoring recruitment to both upper and lower surfaces of artificial plates, it was possible to address the hypothesis that recruitment is greater to downward-facing surfaces than to upward-facing surfaces.

Ideally in recruitment studies all larvae and propagules arriving at the experimental substratum would be counted ('settlement' *sensu* Keough & Downes 1982, Connell 1985). In practice, however, it is generally possible to count only those surviving after the realised sampling interval. Therefore, data from most settlement plate studies incorporate some element of post-settlement mortality. Here, I use the term 'recruitment' to refer to the number of settlers surviving after an immersion period of approximately one month.

MATERIALS AND METHODS

Plate units and sampling procedures

The study sites, equipment, and experimental design are described in detail in previous chapters (Chapters 2 & 4). Briefly; acrylic settlement plates were deployed at 8 m and 20 m depth sites at each of 3 locations (Hangar Cove, South Cove, Anchorage Island). Six replicate plates were deployed at each site, resulting in a total of 36 plates. At monthly intervals throughout one year, all plates were recovered and replaced with fresh plates. All recruits of faunal and algal taxa on the recovered plates were counted and identified to the lowest possible taxonomic level.

The presence of a biofilm has been shown to influence the selection of settlement substratum in some taxa (e.g. Todd & Keough 1994, Harder et al. 2002). Observational tests using the DAPI fluorescence technique to visualise bacteria (Porter & Feig 1980) indicated that an appreciable biofilm developed on plates after immersion for 3-4 days in seawater at ambient temperature. Prior to initial deployment, therefore, all plates were first washed, then conditioned in flowing, 100μm filtered, seawater for a period of not less than 7 days. Prior to each subsequent deployment, plates were abraded to remove all recruits and shell remnants and were again conditioned in filtered seawater for not less than 7 days. On retrieval from the seabed, plates were maintained in

filtered seawater at ambient temperature before being digitally photographed and examined under low-power microscopy (10× to 40×). Examination was conducted in a shallow seawater bath and thus all recruits recorded were alive at the time of census. All recruits present within the central 150 cm^2 analysis area on both upper and lower plate surfaces were recorded on enlarged (A4) negative prints from the whole-plate digital images. By printing these images as negatives, recruits showed as dark marks on a light ground, thus allowing identification codes and image frame numbers to be written directly to a dimensionally accurate map of the plate surface. All taxa were photographed and assigned identification codes, and a reference file of digital images was maintained for each taxon in order to ensure consistency of identifications. Cheilostome bryozoans were identified from Hayward (1995), bivalve molluscs were identified by Dr. K. Linse at the British Antarctic Survey. Other taxa were identified from a range of literature sources or as higher groupings.

Plate deployment

First deployment was in late February 2001 and regular monthly exchanges were conducted until September 2001 when laboratory and dive facilities were destroyed by fire. The study was resumed in late March 2002 and eleven monthly exchanges were conducted from then up to early March 2003 when the final set of plates was retrieved.

Data analysis

Data were recorded as counts of individuals, or individual ancestrulae, recruiting to the central analysis area (150 cm^2) of each plate surface. The range of taxa recruiting to the plates was compared with that recorded on surrounding natural substrata by contrasting the numbers of taxa recorded in each of nine classes of sessile fauna in this study with data from Chapter 3. Total numbers of taxa, and total numbers of individuals per plate surface summed over the eleven sampling points during 2002-3 were analysed by a factorial ANOVA with depth and plate surface as fixed factors, and location as a random factor. Where interactions were significant in this analysis, locations were examined separately. Where the recruitment of individual taxa was seen to vary between plate surfaces depending on the month of immersion, repeated measures ANOVA with month as the repeated measure and surface as a fixed factor was used to determine the significance of month x surface interactions. As *post hoc* tests are not appropriate in repeated measures designs, where interactions were

significant, one-way ANOVAs for the effect of plate surface were run for each month of the period in question. Data distributions were examined graphically prior to analysis (Quinn & Keough 2002) to assess normality of distribution and homogeneity variance. Counts of the numbers of taxa were suitable for analysis without transformation but abundance data required $\log_{10}(x + 1)$ transformation to meet the requirements of the analysis.

Multivariate analyses, using routines within the PRIMER statistical package (PRIMER-e Ltd., Plymouth, UK), were used to examine relationships between depths, locations and month of immersion for all taxa. All multivariate analyses were conducted on fourth-root transformed data in order to down-weight the influence of highly abundant species, and the Bray-Curtis similarity measure was used throughout. Non-metric multi-dimensional scaling (MDS) ordinations were used to visualise relationships between samples, and the taxa contributing most to dissimilarities between groups were identified by the similarities percentages routine (SIMPER). The cyclicity of seasonal patterns was tested using the RELATE correlation procedure. This technique tests for correlations between matrices of Bray-Curtis similarities generated from the sample data, and a model matrix describing a perfectly circular relationship between samples (for rationale of all procedures see Clarke & Warwick 2001, Somerfield et al. 2002).

RESULTS

Sampling

During the entire study, six settlement plates (from a total of 362 individual plate deployments) were destroyed by ice impact. All of these were at 8 m sites: two plates at South Cove in April 2001, and four in Hangar Cove at some point between September 2001 and March 2003. In addition, Anchorage Island sites were inaccessible, because of ice conditions, throughout July and August 2001, and again during May and December 2002. With these exceptions, all plates were exchanged at the turn of each calendar month with a mean immersion period of 32 d (SD 4.9). The inaccessibility of Anchorage resulted in no data from this location for the nominal immersion periods of June, July, and August 2001, and April and November 2002. As a further consequence of this, Anchorage plates retrieved in early June 2002 (May

immersion period) and early January 2003 (December immersion period) had been immersed for 73 d and 61 d respectively, as opposed to mean immersion periods of 31 d and 30 d at the other locations. Assemblages on these plates were qualitatively very similar to those on South Cove plates and standardisation of the number of taxa to a uniform immersion period (by halving all recorded values) was not considered appropriate. Taxonomic data, therefore, have been included without adjustment. Abundances, however, were generally greater across a range of common taxa and counts have been adjusted by a factor of 0.7 . This factor, rather than 0.5, was used to make allowance for post-settlement mortality during the extended immersion period and was estimated from the relative proportions of single ancestrulae versus colonies with developed autozoids in common bryozoan species, particularly *Celleporella antarctica*.

Table 5.1 Immersion periods of short-term recruitment plates. Nominal month labels (second column) are used in all subsequent analyses to simplify presentation. Data from extended immersions (boxed) were not used in analyses except for Anchorage when sea ice was forming ([a])and breaking out ([b]).

		Hangar			South			Anchorage		
Year	Nominal month	deployed	retrieved	days	deployed	retrieved	days	deployed	retrieved	days
2001	Mar	22-Feb	2-Apr	39	13-Feb	23-Mar	38	13-Feb	29-Mar	44
	Apr	2-Apr	27-Apr	25	23-Mar	30-Apr	38	29-Mar	27-Apr	29
	May	27-Apr	13-Jun	47	30-Apr	4-Jun	35	27-Apr	6-Jun	40
	Jun	13-Jun	11-Jul	28	4-Jun	9-Jul	35	6-Jun	...	
	Jul	11-Jul	8-Aug	28	9-Jul	12-Aug	34	...	...	
	Aug	8-Aug	10-Sep	33	12-Aug	12-Sep	31		31-Aug	86
Diving operations suspended		10-Sep	29-Mar	200	12-Sep	2-Apr	202	31-Aug	28-Mar	209
2002	Apr	29-Mar	7-May	39	2-Apr	9-May	37	28-Mar	...	
	May	7-May	7-Jun	31	9-May	10-Jun	32	...	9-Jun	[a]73
	Jun	7-Jun	9-Jul	32	10-Jun	11-Jul	31	9-Jun	14-Jul	35
	Jul	9-Jul	9-Aug	31	10-Jul	12-Aug	33	14-Jul	10-Aug	27
	Aug	9-Aug	8-Sep	30	12-Aug	11-Sep	30	10-Aug	15-Sep	36
	Sep	8-Sep	8-Oct	30	11-Sep	10-Oct	29	15-Sep	12-Oct	27
	Oct	8-Oct	8-Nov	31	10-Oct	10-Nov	31	12-Oct	7-Nov	26
	Nov	8-Nov	10-Dec	32	10-Nov	12-Dec	32	7-Nov	...	
	Dec	10-Dec	9-Jan	30	12-Dec	10-Jan	29	...	7-Jan	[b]61
2003	Jan	9-Jan	5-Feb	27	10-Jan	6-Feb	27	7-Jan	4-Feb	28
	Feb	5-Feb	4-Mar	27	6-Feb	5-Mar	27	4-Feb	3-Mar	27

Taxon identifications

For some taxa, identification to species level of immediate post-settlement individuals was not possible. Thus all sponges, for instance, were grouped under a single heading. In many cases, however, early recruits were distinctive enough that they could be assigned discrete identification codes even though their precise taxonomy could not be determined. Thus, six types of ascidian and two types of cyclostome bryozoan could be discriminated. The cheilostome bryozoan *Notoplites tenuis* (recorded only once) recruited as a fragment of a mature colony, attaching to the plate by means of rhizoids, but all other bryozoans recruited as ancestrulae derived from larvae. The ancestrulae of cheilostome bryozoans are distinctive and the majority of these were identified to species retrospectively by observation of colonies during the production of the first autozooids. Most cheilostome identifications were only confirmed by examination of young colonies on plates which had been left *in situ* for more than one month, especially those left immersed during the six-months of the first year in which diving operations were suspended. A consequence of this is that identifications are more precise for the second year of sampling than for the first. Analyses were, therefore, confined to data from the 2002-3 sampling period, with the exception of year-on-year comparisons of abundances of those species for which identifications were clear from the outset. Where ancestrulae were distinctive but no firm identification could be reached, identification codes were assigned. Ancestrulae at very early stages of development were recorded under the general grouping "indeterminate cheilostomes". Taxon identifications are presented in Appendix A, together with files of representative images on the attached CD (thesis back cover).

Diversity of recruiting taxa

A total of 42 morphologically distinct sessile taxa representing nine phyla were recorded on the plates (Table 5.2). This is a conservative estimate of the actual number of species recruiting, however, as groups such as sponges, cyclostome bryozoans and spirorbid polychaetes are each likely to include several species. Bryozoans were the most speciose group recorded and ancestrulae of 21 cheilostome species were identified. Together with spirorbid polychaetes, bryozoans were also the most abundant group recruiting to plates (Table 5.2). Twenty-eight taxa (67% of the total)

occurred at all three locations, 9 (21%) were recorded at only two locations, and 5 (12%) were recorded at only one location.

The number of taxa recorded in each of the nine principal classes of sessile fauna in the present study (2002-3 data only) are compared with the corresponding numbers of taxa identified on natural substrata at each of the study sites (data from Chapter 3) in Figure 5.1. At this level, recruiting assemblages at all sites appear to be broadly representative of the surrounding biota. Brachiopods (class Articulata) are the only taxon which is completely unrepresented on the settlement plates but the Anthozoa are also under-represented, largely due to the absence of *Alcyonium antarcticum* recruitment to the plates. The apparent paucity of sponge taxa on the settlement plates, however, is probably caused by the inability to distinguish between taxa at very early recruitment stages, as noted above.

Table 5.2 (next page) Sessile taxa recruiting to settlement plates at 20 m and 8 m depths over the period April 2002 to March 2003. Abundance classes for the total number of recruits summed over all months at each site (total surface area per site; 1800 cm^2) are represented by: • 1-9; •• 10-99; ••• 100-999; •••• 1000-9999; ••••• ≥10000.

			Location and depth					
			Hangar		South		Anchorage	
Phylum	Class	Taxon	20 m	8 m	20 m	8 m	20 m	8 m
Porifera	Demospongiae	Sponges	••	•••	••		••	
Rhizopoda		Foraminiferans	•	••	••	••	•••	••
Ciliophora	Polyhymenophora	*Folliculina* spp.	•		••	•••	•••	••
Cnidaria	Hydroida	Hydrozoans	•••	••	••	••	•••	•
	Alcyonaceae	*Primnoella* sp.					•	
		Indet. cnidarian [CD5_8.02]					•	
Annellida	Polychaeta	Serpulids	•••	••	•••	••	••	••
		Spirorbids	•••••	••••	•••••	••••	••••	••••
Mollusca	Bivalvia	*Adamussium colbecki*	••		••	•	••	
		Philobrya sublaevis			•		•	
Bryozoa	Stenolaemata	Cyclostome 1	••	••	•••	••	••••	••
		Cyclostome 2	•••	••	••	•••	••	••
	Gymnolaemata	*Aimulosia antarctica*	••	•	•••	•••	•••	•••
		Hippadanella inerma	•		•	•	•	
		Arachnopusia inchoata	••	••	••	•	••	•
		Chaperiopsis protecta	••	•••	••	•	••	•
		Fenestrulina rugula	••••	••••	•••	•••	•••	•••
		Micropora notialis	•••	•••	•	••	•	•
		Micropora brevissima		•		•		
		Celleporella antarctica	••	••	••••	••••	••••	•••
		Celleporella dictyota			•	•		
		Celleporella bouganvillei	•		••	•	••	••
		Beania erecta	•	••	•	•	••	••
		Camptoplites bicornis	••	•	•	•	••	•
		Osthimosia sp.					••	
		Figularia discors			•		•	
		Smittina sp.	••	•	•	•		•
		Ellisina antarctica	••	••	••	••	•••	••
		Lageneschara lyrulata	••	•	•			
		Notoplites tenuis					•	
		Inversiula nutrix	•				•	•
		Erect cheilostome 2	•		•		•	
		Erect cheilostome 4			•		•	
		Indet. ancestrula type 5			•		•	
		Indet. cheilostomes	••	••	••	••	•••	••
Chordata	Ascidacea	Solitary Ascidian 1	••	•	•••	••	•••	••
		Solitary Ascidian 2	••	•	••	•	••	••
		Solitary Ascidian 3			•	•	••	
		Solitary Ascidian 4	••		••		••	
		Solitary Ascidian 5			•	•	•	•
		Compound Ascidian 1	••	•	•	•	••	•
Rhodophyta	Florideophyceae	Coralline algae	•••	••	•••	••	•••	••

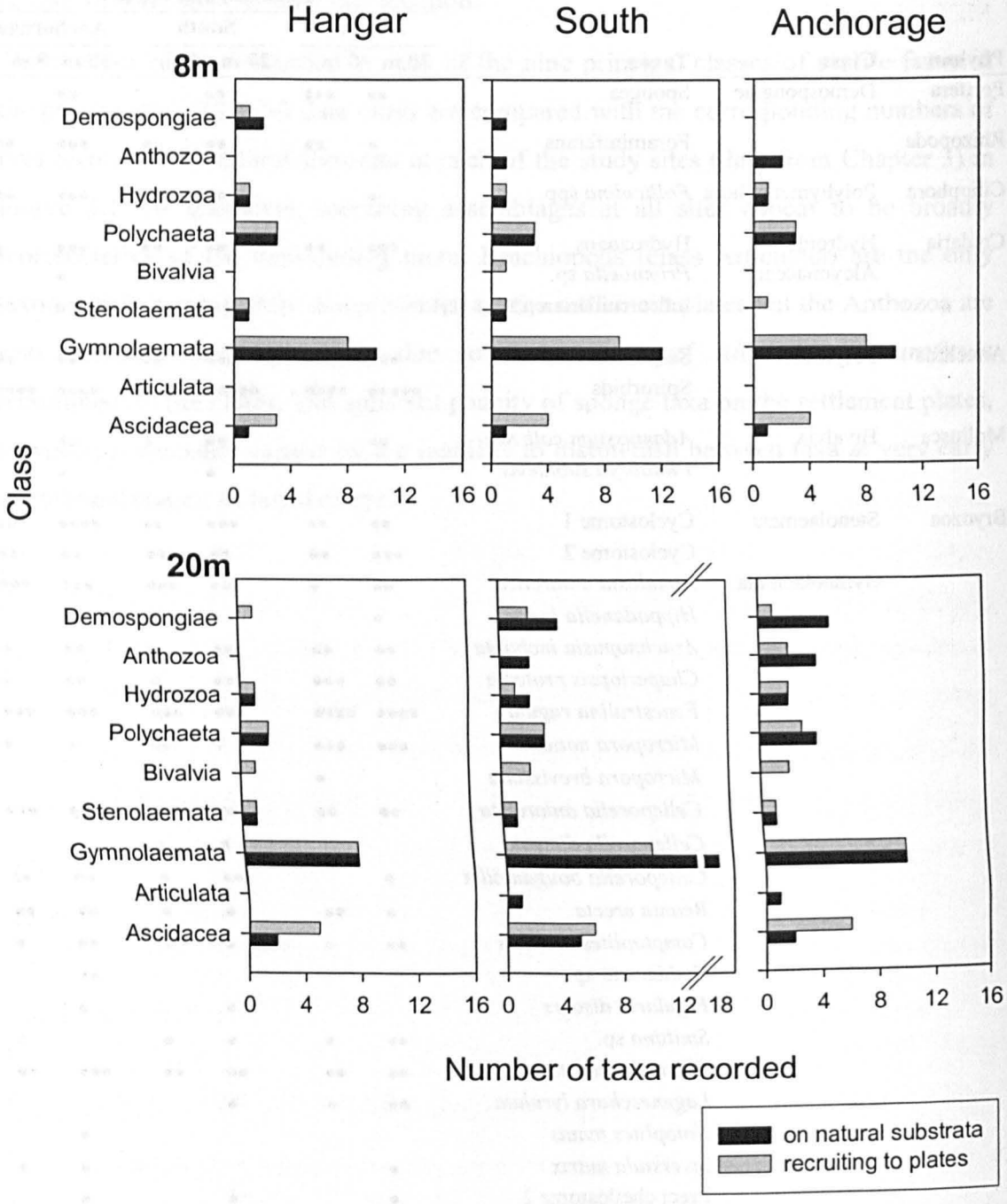


Figure 5.1 Numbers of taxa recorded on natural substrata (black bars) and recruiting to artificial substrata (grey bars) in the nine major classes of sessile macrofauna present in the study area. Natural substrata data are from Chapter 3, recruitment data are from 2002-3 in the present study.

Seasonal patterns of recruitment

MDS ordinations of Bray-Curtis similarities between the average assemblage recruiting in each month show a cyclical progression through the eleven months of the second year of the study at each location × depth combination (Figure 5.2). Thus, late summer assemblages recruiting in February 2003 were more similar to late summer assemblages recruiting in April 2002 than to those recruiting in the intervening winter or early summer. Correlations of the similarity matrices underlying these ordinations with a model matrix representing an idealised circular relationship between samples (RELATE procedure in PRIMER) are significant ($P < 0.001$) in all cases, suggesting that the assemblages recruiting through the year follow a predictable annual pattern.

Comparisons of the mean number of taxa recruiting per surface in each month (Figure 5.3) show that recruitment took place throughout the year but that patterns were not consistent across locations. Hangar Cove assemblages exhibited a distinct seasonality of recruitment, with greater mean numbers of taxa recruiting in the summer months (Nov-Feb) and a mid-winter (Jun-Jul) minimum. South Cove recruitment was more uniform throughout the year with poorly defined trends towards a summer maximum at 8m and a winter maximum at 20m. Anchorage recruitment at 20m showed a pronounced late-winter (Jul-Sep) maximum, with the highest mean taxon richness recorded at any site, for any month (14.3 ± 1.05 mean±se), recruiting to upper plate surfaces during August. In plots of the total number of taxa recruiting per month (Figure 5.3 bold line), this late winter pulse of recruiting taxa was evident at all 20m sites but was not clear at 8m sites. SIMPER analyses comparing recruitment in winter (Jun-Aug) with that in summer (Dec-Feb) (Table 5.3) indicated that the winter peak was associated with a range of taxa including solitary ascidians, cheilostome bryozoans, cnidarians and thecate protozoans, many of which recruited in low abundances and thus exerted little influence on the mean values plotted in Figure 5.3.

Monthly abundances of individual species and taxa (Figure 5.4, Figure 5.5) show distinct seasonality of recruitment in most cases and, where data from the two sampling periods overlap, there is evidence that recruitment patterns were similar in consecutive years. Across the range of taxa sampled, there are examples of both year-round and highly seasonal recruitment, and of peak recruitment taking place in all months of the year other than June (mid-winter). Peak recruitment of individual

cheilostome bryozoan species, with the exception of *Celleporella* sp. and *Aimulosia antarctica*, was generally restricted to periods of one or two months and, in all species, took place in the period from July to January, encompassing the second half of the winter through to midsummer. Peak recruitment of all ascidian species also occurred during this period: of the six species recorded, four recruited in winter and two in midsummer.

Figure 5.5 shows recruitment of eight cheilostome bryozoan species grouped by their rankings in a hierarchy of competitive overgrowth abilities as determined by Barnes & Rothery (1996) for bryozoan assemblages at Signy Island. The left panel shows recruitment of four strongly competitive species and the right panel shows recruitment of four weakly competitive species. Within each panel, species are further ranked from top to bottom in order of decreasing competitive ability (Barnes & Rothery 1996 and Barnes pers comm). Comparison of peak recruitment periods in relation to the mid-summer datum (dotted line) shows that the group of weaker competitors recruited earlier in the year than did the stronger competitors.

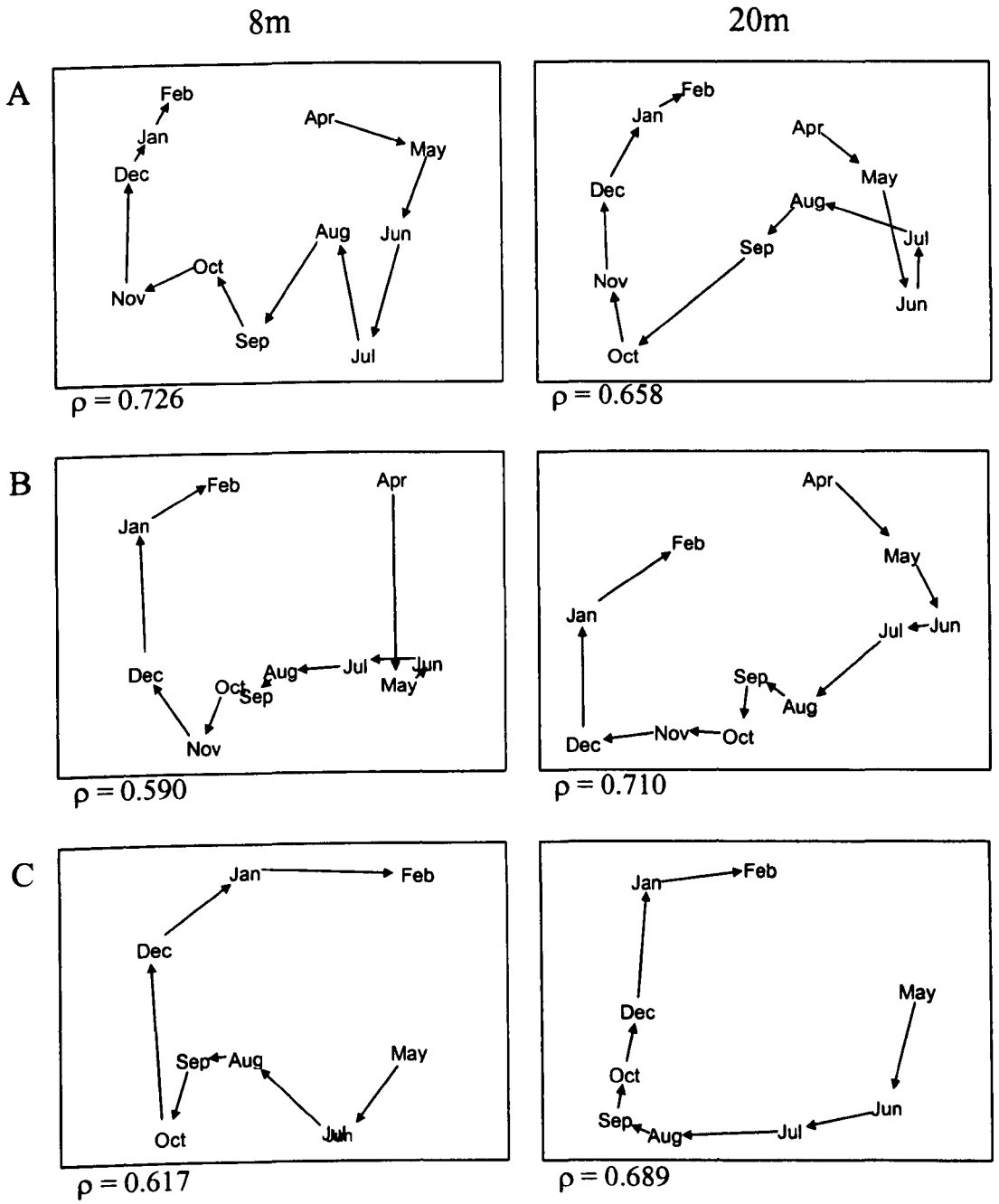


Figure 5.2 MDS ordinations of monthly recruitment to settlement plates at Hangar Cove (A), South Cove (B), and Anchorage (C) from April 2002 to February 2003. Plots represent the monthly average assemblage recruiting to both surfaces of all plates for each depth at each location. Underlying matrices of Bray-Curtis similarity are derived from recruitment data for all taxa averaged by site and fourth-root transformed. RELATE values (ρ) are shown for the strength of correlations with an idealized cyclical matrix. All correlations are significant at $P < 0.001$, indicating that recruiting assemblages follow a predictable annual pattern. Stress values are ≤0.06 for all ordinations.

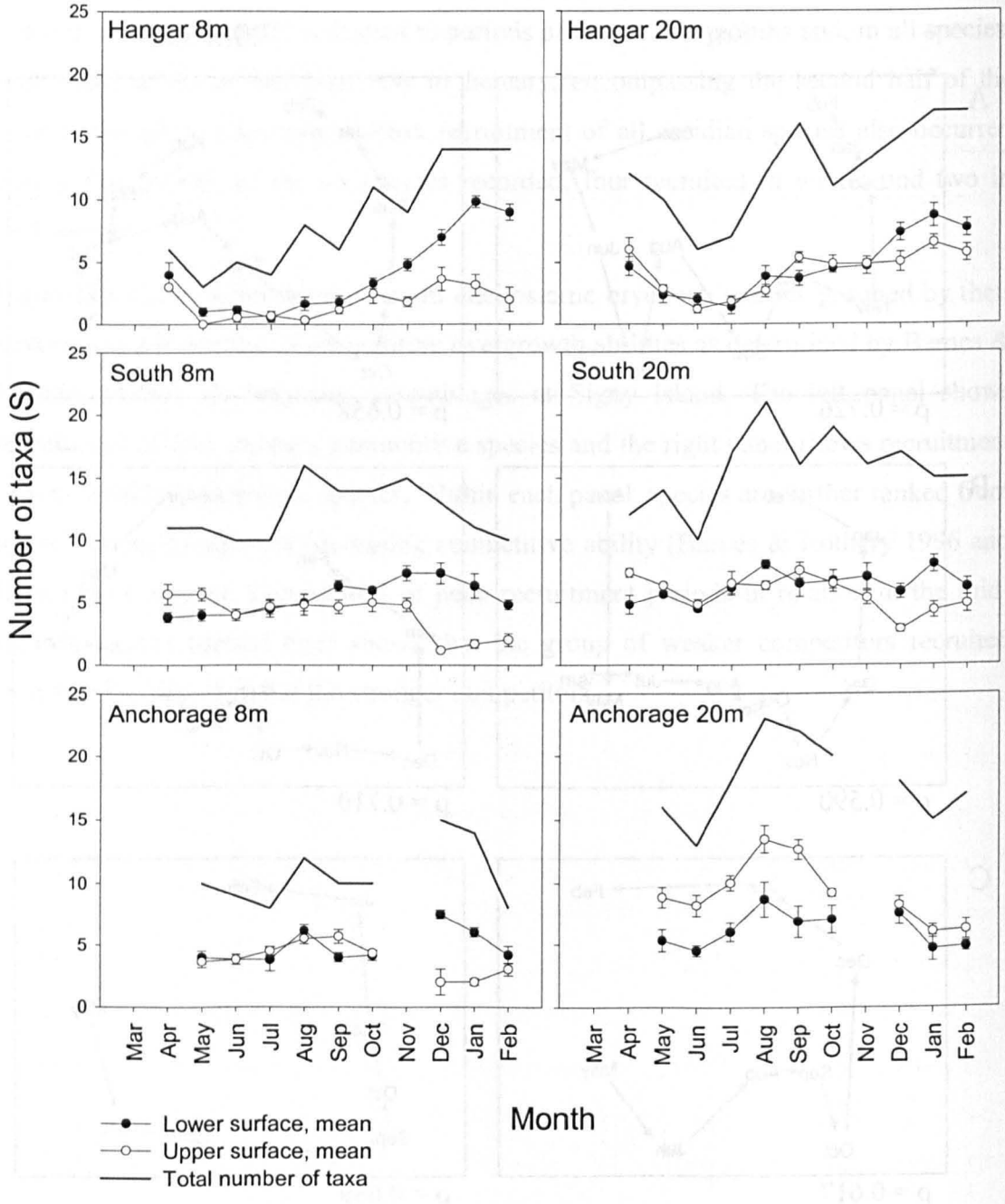


Figure 5.3 Total numbers of faunal taxa (species and other taxa: Table 1) recruiting at each study site, and mean numbers of taxa recruiting to upper and lower surfaces of settlement plates at two depths (8 m, 20 m) and 3 locations (Hangar, South, Anchorage) between April 2002 and February 2003. Plates were immersed for 32 ± 4.9 (mean ± sd) days. Plotted values are means, error bars are 1SE, n = 6. (Note: Anchorage data for May and December are from plates immersed for 73d and 61d respectively).

Table 5.3 Taxa contributing to the dissimilarity between assemblages recruiting in summer (Dec-Feb) and winter (Jun-Aug) with indication of taxa recruiting only in summer (○) or only in winter (•). Taxa are in order of decreasing contribution to overall dissimilarity between seasons in a SIMPER analysis based on presence/absence transformed data. Abundance data (average number of recruits 150cm^{-2} across all locations and depths) are given as untransformed values.

Taxon		Average number of recruits 150cm^{-2}		Average dissimilarity	Dissim. / SD
Summer taxa		Jun-Aug	Dec-Feb		
Serpulids	○	0.00	2.71	3.61	0.74
Micropora notialis		0.03	1.67	2.72	0.65
Solitary ascidian 1		0.13	0.51	2.10	0.51
Arachnopusia inchoata		0.02	0.57	1.81	0.53
Chaperiopsis protecta		0.06	0.70	1.59	0.50
Sponges		0.08	0.87	1.49	0.40
Beania erecta	○	0.00	0.58	1.43	0.44
Compound ascidian 1	○	0.00	0.20	0.98	0.36
Smittina sp.		0.02	0.10	0.65	0.28
Adamussium colbecki	○	0.00	0.08	0.31	0.19
Lageneschara lyrulata	○	0.00	0.01	0.04	0.07
Winter taxa					
Celleporella antarctica		15.75	1.22	5.70	0.92
Solitary ascidian 5		0.49	0.02	2.80	0.56
Hydrozoans		0.51	0.07	2.19	0.46
Folliculina spp.	•	0.95	0.00	1.78	0.46
Solitary ascidian 2		0.19	0.03	0.61	0.30
Osthimosia sp.		0.22	0.02	0.51	0.28
Figularia discors	•	0.07	0.00	0.35	0.23
Solitary ascidian 3	•	0.13	0.00	0.31	0.22
Solitary ascidian 4		0.18	0.01	0.30	0.21
Philobrya sublaevis	•	0.04	0.00	0.17	0.14
Indet cheilostome 5	•	0.03	0.00	0.15	0.15
Erect cheilostome 2	•	0.04	0.00	0.14	0.16
Indet cheilostome 6	•	0.01	0.00	0.08	0.10
Inversiula nutrix	•	0.01	0.00	0.07	0.10
Notoplites tenuis	•	0.01	0.00	0.04	0.07
Indet. Cnidarian	•	0.01	0.00	0.03	0.07
Primnoella sp.	•	0.02	0.00	0.02	0.07

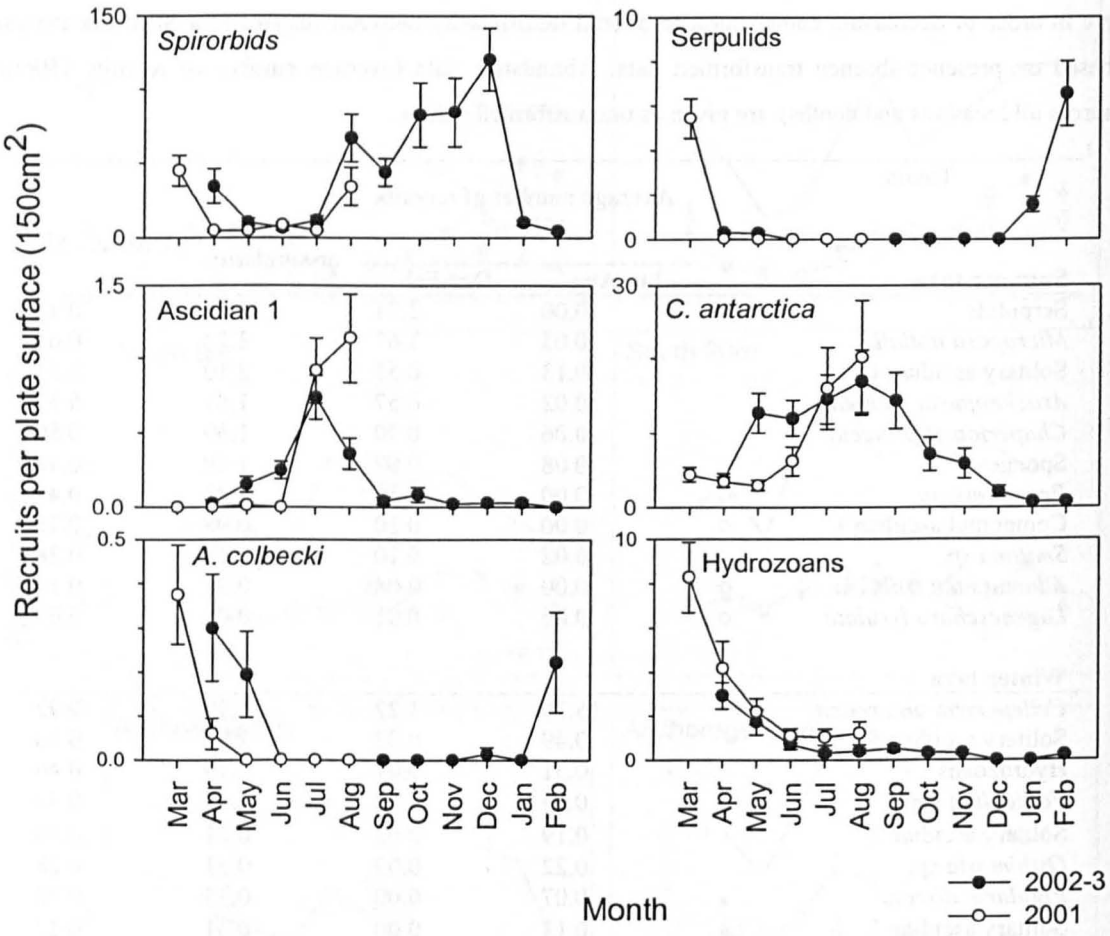


Figure 5.4 Recruitment of selected sessile taxa to settlement plates during the years 2001 and 2002-3. Data are means across all locations, depths, and surfaces, n = 72, except Jun-Aug 2001 and Apr and Dec 2002 n = 48, error bars 1SE.

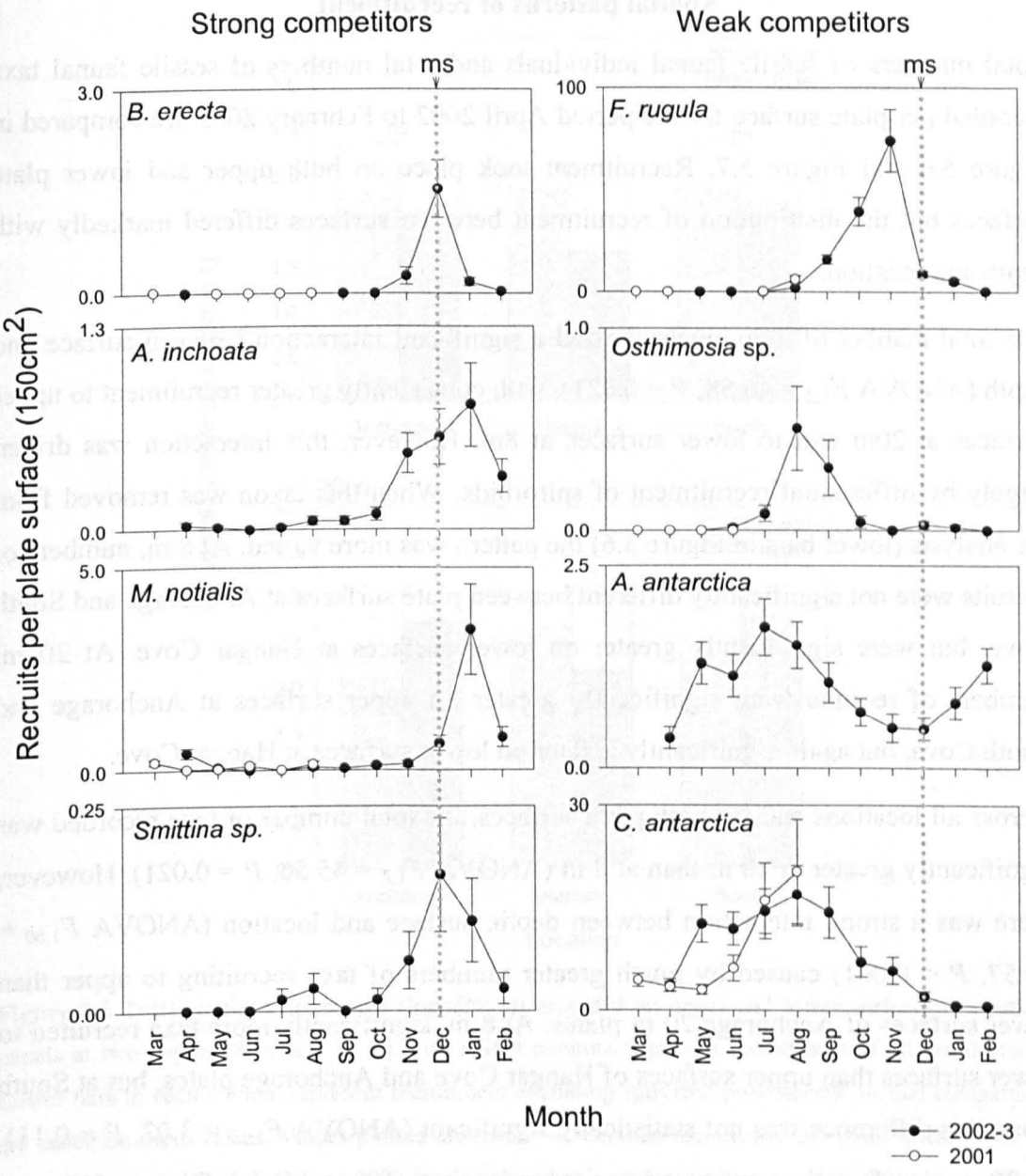


Figure 5.5 The timing of peak recruitment period in relation to overgrowth competition strength for selected cheilostome bryozoan species. The left and right panels, respectively, show recruitment of four strongly competitive, and four weakly competitive species. Within each panel, species are ranked from top to bottom in order of decreasing competitive ability (rankings follow the hierarchy of overgrowth competition strength in Barnes & Rothery 1996). The dotted lines "ms" indicate midsummer. Where reliable identifications were available in the first year of the study, data for both 2001 and 2002-3 are shown. Data are means across all locations, depths, and plate surfaces, n = 72, except Jun-Aug 2001 and Apr and Dec 2002 n = 48, error bars 1SE.

Spatial patterns of recruitment

Total numbers of sessile faunal individuals and total numbers of sessile faunal taxa recorded per plate surface for the period April 2002 to February 2003 are compared in Figure 5.6 and Figure 5.7. Recruitment took place on both upper and lower plate surfaces but the distribution of recruitment between surfaces differed markedly with depth and location.

The total number of individuals showed a significant interaction between surface and depth (ANOVA $F_{1,2} = 46.58$, $P = 0.021$), with consistently greater recruitment to upper surfaces at 20m and to lower surfaces at 8m. However, this interaction was driven largely by differential recruitment of spirorbids. When this taxon was removed from the analysis (lower bars in Figure 5.6) the pattern was more varied. At 8 m, numbers of recruits were not significantly different between plate surfaces at Anchorage and South Cove, but were significantly greater on lower surfaces at Hangar Cove. At 20 m, numbers of recruits were significantly greater on upper surfaces at Anchorage and South Cove, but again significantly greater on lower surfaces at Hangar Cove.

Across all locations and for both plate surfaces, the total number of taxa recorded was significantly greater at 20 m than at 8 m (ANOVA $F_{1,2} = 45.56$, $P = 0.021$). However, there was a strong interaction between depth, surface and location (ANOVA $F_{1,60} = 10.57$, $P < 0.001$) caused by much greater numbers of taxa recruiting to upper than lower surfaces of Anchorage 20 m plates. At 8 m, significantly more taxa recruited to lower surfaces than upper surfaces of Hangar Cove and Anchorage plates, but at South Cove this difference was not statistically significant (ANOVA $F_{1,10} = 3.02$, $P = 0.11$). At 20 m, significantly more taxa recruited to lower surfaces of South Cove and Hangar Cove plates, but at Anchorage significantly more taxa recruited to upper surfaces.

Thus, while significantly more taxa recruited at 20 m than at 8 m, there was no clear generality of pattern across locations in either the total number of individuals or the total number of taxa recruiting to upper and lower plate surfaces. However, even where differences between surfaces were statistically significant, it is clear that recruitment to both surfaces was substantial in terms of both numbers of taxa and numbers of individuals.

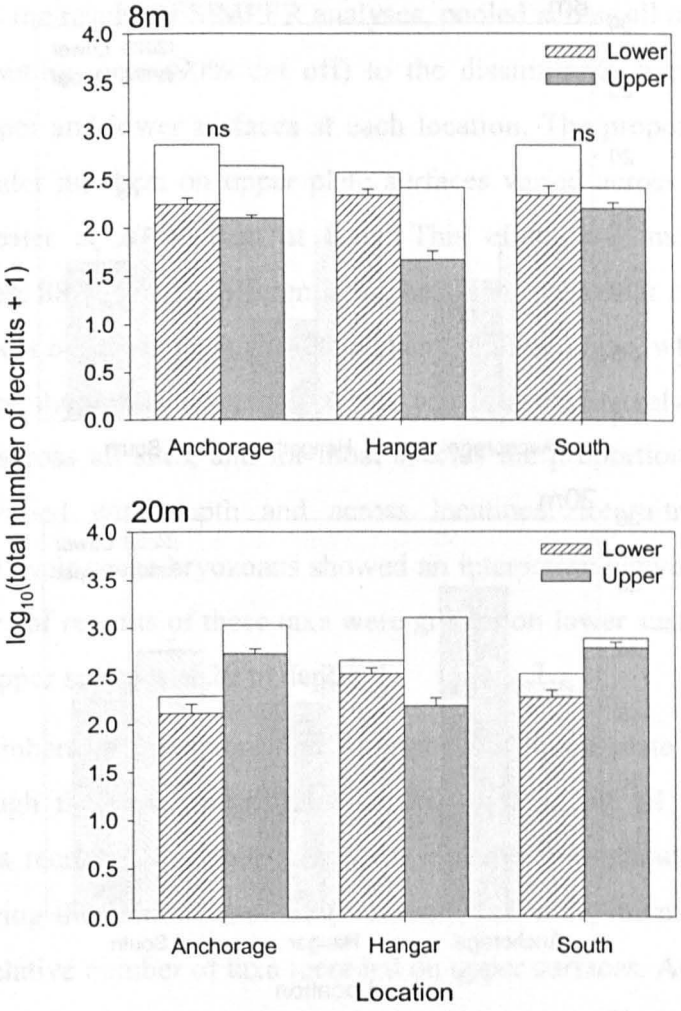


Figure 5.6 Total numbers of recruits ($\log_{10}(N+1)$) recorded on upper and lower surfaces of artificial panels at two depths (8 m and 20 m). Full height columns represent recruitment of all sessile fauna. Lower bars in each column represent recruitment excluding spirorbid polychaetes: formal comparisons are based on these values. Values plotted are means of summed recruitment per plate surface over the period March 2002 to February 2003 excluding April and November, ns indicates non-significant differences (ANOVA $P > 0.05$) for comparisons excluding spirorbids, (n = 6, error bars 1SE). Error bars for full height columns are omitted for clarity but are <0.15 in all cases.

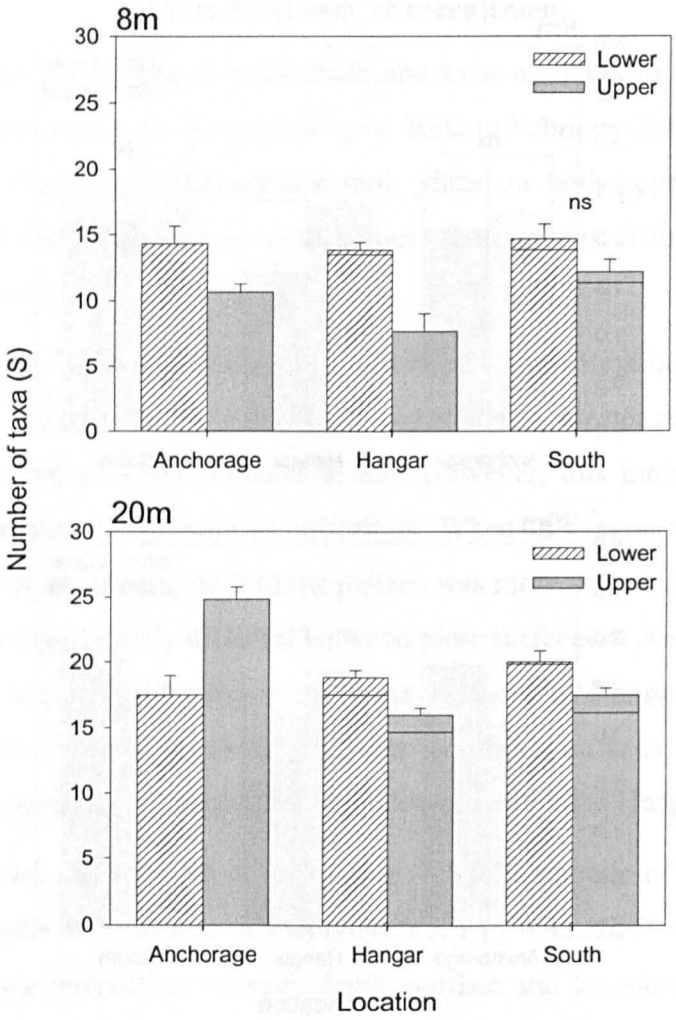


Figure 5.7 Total numbers of taxa recorded on upper and lower surfaces of artificial panels at two depths (8 m and 20 m) over the period March 2002 to February 2003. Crossbars on Hangar and South plots indicate mean total number of taxa excluding data from April and November 2003 to show comparisons with Anchorage, for which there are no data in these months. Error bars on these values are omitted for clarity but are <1.4 in all cases. ns indicates non-significant differences (ANOVA $P > 0.05$) n = 6, error bars 1SE. Full data are used in formal comparisons between plate surfaces.

Table 5.4 shows the results of SIMPER analyses, pooled across all months, identifying the taxa contributing most (90% cut off) to the dissimilarity between assemblages recruiting to upper and lower surfaces at each location. The proportion of these taxa recorded in greater numbers on upper plate surfaces varied across locations but was consistently greater at 20 m than at 8 m. This effect was most pronounced at Anchorage, where 88 % of taxa differentiating between surfaces at 20 m were recorded in greater numbers on upper surfaces. Other than coralline algae, which recruited only to upper surfaces, there were no species which recruited exclusively to either upper or lower surfaces across all sites, and for most species the proportion of recruitment to each surface varied with depth and across locations. Recruitment of spirorbid polychaetes and cyclostome bryozoans showed an interaction between depth and plate surface: numbers of recruits of these taxa were greater on lower surfaces at 8 m depth, but greater on upper surfaces at 20 m depth.

The relative numbers of taxa recruiting to upper and lower plate surfaces were not consistent through the year (means plots in Figure 5.3). At all 8 m sites, similar numbers of taxa recruited to upper and lower surfaces throughout the winter period (May-Oct). During the summer months (Nov-Jan), however, there was a pronounced decline in the relative number of taxa recorded on upper surfaces. At 20 m, this pattern was not clear and recruitment to upper and lower surfaces at Hangar Cove and South Cove was generally similar throughout the year. At the Anchorage 20 m site, however, the numbers of recruiting taxa recorded were significantly higher on upper surfaces in all but one (Dec) of the nine months sampled.

Examination of individual species' abundances showed that the decrease in taxa recruiting to upper plate surfaces at 8m during the summer months at South Cove and Anchorage (Figure 5.3) was associated with declines in the abundances of several taxa. This effect was most pronounced for hydroids, coralline algae, cyclostome bryozoans, *Ellisina antarctica*, *Camptoplites bicornis*, and *Fenestrulina rugula*. To illustrate this, Figure 5.8 shows the relative abundance of *F. rugula* recruits recorded on upper and lower plate surfaces in South Cove during 2002-3. From August to October, at both depths, recruitment to upper surfaces was not significantly different from, or was greater than, recruitment to lower surfaces (one way ANOVA, $P > 0.1$ in all cases except August 20 m, $P = 0.049$). However, from November to January at 8 m, and

from November to December at 20 m, recruitment to upper surfaces was significantly less than that to lower surfaces ($P < 0.02$ in all cases).

Table 5.4 SIMPER analysis of the taxa contributing most (90 % cut-off) to dissimilarity between assemblages recruiting to upper and lower surfaces of settlement plates (150 cm^2) at 8 m and 20 m depths. Data are averages from 6 plates over 11 (Hangar Cove and South Cove) or 9 (Anchorage) monthly sampling points from April 2002 to February 2003. Dissimilarity/SD is a relative measure of how consistent each taxon's contribution to overall dissimilarity is across all samples. Taxa recruiting predominantly to upper surfaces are indicated (•). Abundances are given as untransformed values but in order to downweight the influence of more abundant taxa, data were fourth-root transformed for analysis of relative contributions to dissimilarity.

Site	Taxon		Average number of recruits $150cm^{-2}$		Average dissimilarity	Dissim. / SD
			Upper	Lower		
Hangar Cove						
8 m	Spirorbids	•	31.93	18.98	15.6	1.17
	Fenestrulina rugula		11.14	25.23	14.46	0.91
	Cyclostome 2		0.64	1.38	5.17	0.77
	Sponges		0.19	3.42	5.17	0.83
	Hydroids	•	0.98	0.00	4.87	0.48
	Micropora notialis		0.33	4.79	4.63	0.86
	Chaperiopsis protecta		0.05	2.35	3.73	0.82
20 m	Spirorbids	•	154.22	15.61	10.94	1.10
	Fenestrulina rugula		16.94	52.27	10.10	1.00
	Hydroids	•	1.66	0.00	5.05	0.86
	Cyclostome 2	•	2.02	1.72	4.75	0.89
	Celleporella antarctica	•	0.65	0.30	4.18	0.67
	Coralline algae	•	1.95	0.00	3.76	0.76
	Micropora notialis	•	1.09	0.48	3.47	0.86
	Serpulids		0.32	4.66	2.88	0.58
	Cyclostome 1	•	0.78	0.36	2.86	0.70
	Aimulosia antarctica		0.14	0.25	2.31	0.48
	Arachnopusia inchoata		0.17	0.70	2.04	0.63
South Cove						
8 m	Spirorbids		15.47	59.73	7.94	1.29
	Celleporella antarctica	•	10.17	7.97	6.75	1.15
	Fenestrulina rugula		4.63	6.35	6.37	1.04
	Cyclostome 2		0.82	2.00	4.80	1.06
	Aimulosia antarctica		0.60	1.72	4.49	1.03
	Folliculina sp. 1		0.13	5.13	3.88	0.64
	Ellisina antarctica		0.15	0.82	3.64	0.92
	Cyclostome 1		0.30	1.05	3.07	0.67

20 m	*Celleporella antarctica*	•	50.27	3.36	7.95	1.56
	Coralline algae	•	7.67	0.00	6.67	1.36
	Spirorbids	•	19.00	17.05	5.09	1.22
	Fenestrulina rugula		3.77	5.02	4.51	1.01
	Cyclostome 1	•	5.61	4.62	4.21	1.10
	Aimulosia antarctica		1.24	2.42	4.03	1.11
	Hydroids	•	0.89	0.03	2.44	0.79
	Cyclostome 2		0.42	0.44	2.40	0.76
	Serpulids		0.41	1.42	2.35	0.63
	Ascidian 1		0.05	1.20	2.10	0.67
	Folliculina sp. 1		0.21	0.73	1.98	0.62
	Chaperiopsis protecta		0.05	0.53	1.91	0.71
Anchorage						
8 m	Spirorbids		37.72	64.07	9.93	1.37
	Fenestrulina rugula		5.83	12.56	7.86	1.01
	Celleporella antarctica	•	5.15	1.48	6.58	1.22
	Aimulosia antarctica		0.92	1.35	5.05	1.06
	Cyclostome 1		0.72	1.06	4.58	0.99
	Coralline algae	•	1.43	0.00	3.99	0.72
	Ellisina antarctica		0.34	0.46	3.09	0.74
	Ascidian 5		0.06	0.30	2.21	0.59
20 m	Coralline algae	•	11.89	0.00	6.23	1.59
	Spirorbids	•	70.74	9.48	5.52	1.33
	Celleporella antarctica	•	20.74	1.46	4.98	1.48
	Cyclostome 1	•	17.13	4.20	3.93	1.13
	Foraminiferans	•	1.93	0.02	3.34	1.18
	Ellisina antarctica	•	2.87	2.04	3.09	1.08
	Fenestrulina rugula	•	2.67	1.04	2.84	0.98
	Aimulosia antarctica	•	2.74	1.37	2.57	0.97
	Hydroids	•	2.76	0.00	2.42	0.73
	Ascidian 1		0.13	1.06	2.20	0.85
	Camptoplites bicornis	•	1.46	0.24	2.20	0.84
	Serpulids	•	0.72	0.44	1.70	0.59
	Osthimosia sp.	•	0.81	0.50	1.65	0.74
	Folliculina sp. 1	•	1.43	0.70	1.53	0.54
	Ascidian 5		0.31	0.48	1.44	0.65

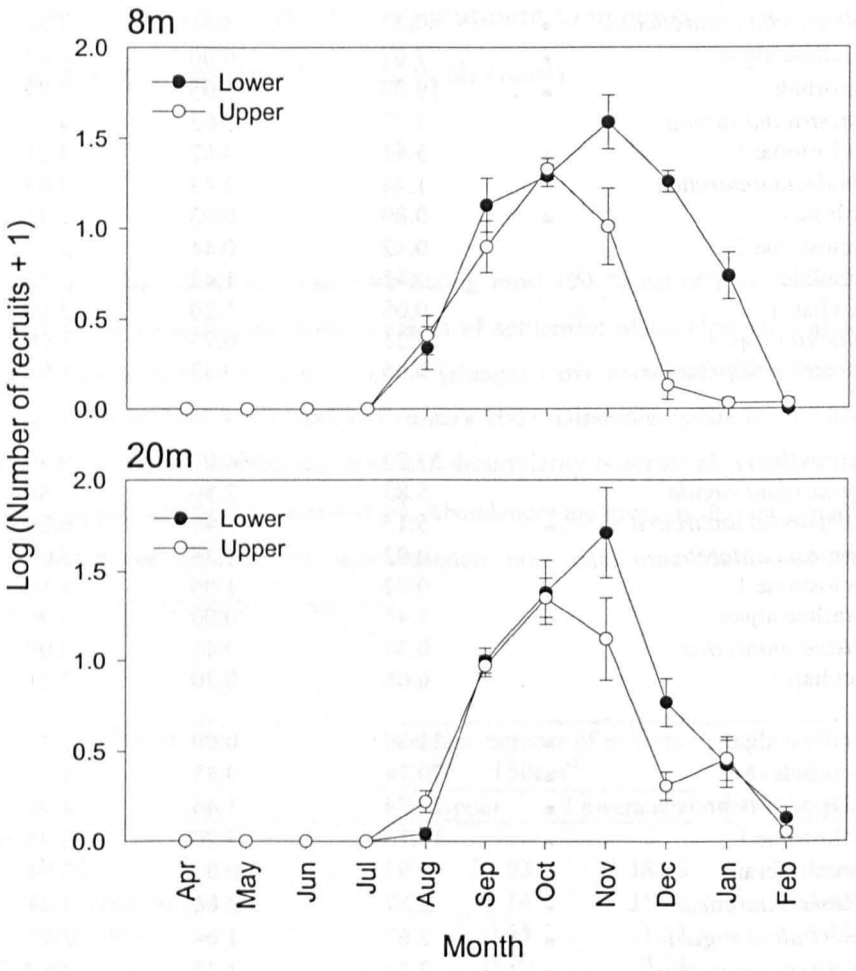


Figure 5.8 *Fenestrulina rugula.* Recruitment to upper and lower surfaces of settlement plates at two depths in South Cove, illustrating the difference in numbers of recruits to upper and lower surfaces from November to January at 8 m, and from November to December at 20 m. In these months there were significantly fewer recruits recorded on upper than lower surfaces at both depths (ANOVA, $P < 0.05$ in all cases). n = 6, error bars 1se.

DISCUSSION

These data show that recruitment of sessile invertebrates to hard substrata in a near-shore Antarctic location took place throughout the year. However, most taxa exhibited pronounced seasonality of recruitment and, when viewed overall, recruiting assemblages followed a cyclical pattern through the year, suggesting an annual pattern of reproduction for most taxa. For many taxa, the period of recruitment did not coincide with the summer pulse of primary production and many recruited during winter. Therefore, the hypothesis that recruitment of the majority of taxa coincides with the period of maximum food availability is not supported. The results also show that more taxa recruited at 20 m than at 8 m, and that total recruitment to upward-facing surfaces was substantial and comparable with that to downward-facing surfaces. Thus, the data support the hypothesis that the diversity of recruitment decreases with decreasing depth, but do not support the hypothesis that there is greater recruitment to downward-facing surfaces.

For the majority of taxa recorded, the present data suggest an annual cycle of reproduction and recruitment (Figure 5.2). The relatively short duration of the study, however, does not allow it to discount the possibility of significant inter-annual variability, or of episodic recruitment events, as described by Dayton (1989) for the sponge *Homaxinella balfourensis* in McMurdo Sound. Although recruitment to artificial substrata in the present study appears to be broadly representative of sessile assemblages in the area (Figure 5.1), some sessile species known to be present at the experimental locations (Chapter 3) were not recorded on the settlement plates. While this might be as a result of larval settlement preferences, patchy distributions, or restricted dispersal, it is also possible that the reproductive cycles of these species are not annual, or that the supply of larvae is affected by non-annual physical fluctations.

Considering the extreme seasonality of primary production in high-latitude marine environments (Arntz et al. 1994, Clarke & Leakey 1996), it is perhaps surprising that there is no evidence of a single optimal period for reproduction amongst the sessile suspension-feeding taxa recorded here. Indeed, when compared simply in terms of the total number of taxa recruiting, assemblages in temperate latitudes appear to show more pronounced seasonality and synchronisation with the summer bloom than do the high latitude assemblages studied here. Moreover, peak taxon richness at 20 m in the

present study was recorded in winter. Although, worldwide, there are few studies with comparable year-round sampling, and none at comparable depths, data from three recruitment studies in the immediate sublittoral in the North Atlantic (Figure 5.9) suggest that this is the opposite of the pattern seen in temperate assemblages.

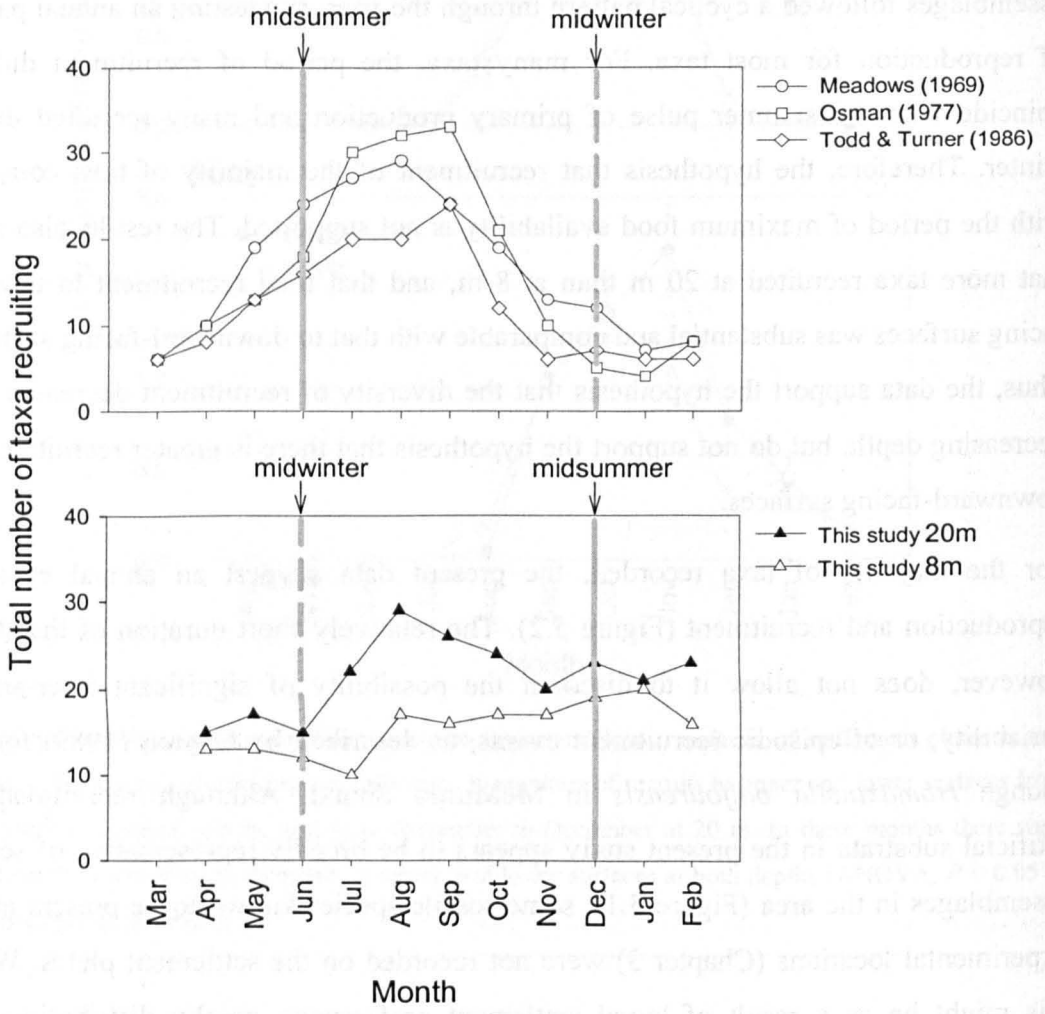


Figure 5.9 Comparison of the total numbers of sessile faunal taxa recruiting per month to artificial plates in three northern hemisphere temperate sublittoral studies (top) and in the present study (bottom). The months of midwinter and midsummer are indicated, contrasting the post midsummer peak of recruitment in the temperate latitude studies with a post midwinter peak at 20 m in this study. Values plotted are totals per month in each study. Depths in the temperate studies range from 1 m to 3 m below mean low water.

Most of the taxa recruiting in this study, notably bryozoans, ascidians and sponges, reproduce by means of non-feeding, lecithotropic larval stages (Hayward 1995, Todd 1998, Young 2002) and their spawning might thus be expected to be decoupled to

some extent from the summer pulse of primary productivity. As these taxa share similar feeding modes and are of similar sizes at settlement, however, it might still be predicted that there would be a common optimal time of settlement. However, peak recruitment periods of cheilostome bryozoans and ascidians recorded in this study are distributed from mid-winter through to late summer, and may be either brief or extended. For cheilostome bryozoans, a similar recruitment period has been reported in the maritime Antarctic (Stanwell-Smith & Barnes 1997), and the common Antarctic ascidian *Cnemidocarpa verrucosa* has been shown to spawn in winter at King George Island (Sahade et al. 2004), suggesting that these patterns may be general in Antarctic waters and thus that the summer phytoplankton bloom is not the principal cue for reproduction in these taxa.

This, in turn, suggests that the months of the Antarctic winter may not be as limiting to survival as might be thought. There are two lines of research which may combine to explain this. Firstly, physiological studies of vagile benthic species in the Antarctic have shown that very low resting metabolic rates resulting from low seawater temperatures enable overwintering with negligible loss of tissue mass (Brockington 2001b, Brockington & Clarke 2001). Thus, the energetic cost of survival following winter settlement in sessile species may also be very low. Secondly, it has been demonstrated that several species of Antarctic bryozoan feed for all but a short period (~2-3 months) of the year (Barnes & Clarke 1995), utilising the nanoplanktonic fraction (2-20 μm) of primary production which persists at low levels through the winter months (Clarke & Leakey 1996). Similarly, the winter-spawned planktotrophic larvae of the asteroid *Odontaster validus*, and the nemertean *Parborlasia corrugatus*, both abundant in Antarctic coastal waters, have been shown to feed and grow through the winter months on this fraction of primary productivity (Rivkin et al. 1986, Bosch & Rivkin 1988, Pearse et al. 1991a). Thus, food-limitation does not appear to be a critical restriction for bryozoans or larvae during the austral winter, and, by extension, may not be for the smallest juvenile stages of other sessile suspension-feeding organisms. Adult solitary ascidians, for instance, consume a wide range of food particle sizes from ~1μm upwards (Randlov & Riisgard 1979, Bingham & Walters 1989, Kowalke 1999), but recently-metamorphosed juveniles are too small to take in the larger phytoplankton cells which are characteristic of the austral summer bloom. Nanoplankton is, therefore, likely to be a significant food source for ascidians during the immediate post-

settlement period and, thus, there may be no nutritional disadvantage to winter settlement. That four out of the six ascidian types recorded here recruited exclusively in winter lends weight to this argument.

More compelling adaptive reasons for recruitment to take place during the winter might be found in greater availability of free substratum and reduced mortality at this time of year; both factors being principally related to the activities of macrobenthic grazers, and suspension and deposit feeders. Nearshore Antarctic waters support high abundances of such taxa (Kirkwood & Burton 1988, Dayton 1990, Arntz et al. 1994, Barnes & Brockington 2003). During the summer bloom the seabed at shallower depths is dominated by limpets and urchins, while below ~15 m extensive areas are covered by the feeding tendrils of terebellid polychaetes and holothurians. In the present study, urchins, limpets, and asteroids were numerous on plate upper surfaces, while holothurians, terebellids and nemerteans were often found inhabiting the space between plate undersurfaces and the base panel. These taxa are active during the highly productive months of the summer bloom but many, particularly the suspension and deposit feeders and the urchin *S. neumayeri*, are largely inactive through the rest of the year (Brockington et al. 2001 and pers obs). The probability of a settling larva encountering clear substratum, and subsequently avoiding death by grazing or smothering, is consequently higher in winter than in summer.

Ice-mediated disturbance of the seabed, which is responsible for considerable mortality of benthic fauna in polar seas (Gutt et al. 1996, Barnes 1999, Peck et al. 1999, Gutt 2001, Brown et al. 2004), is also reduced or absent in winter when the surface waters freeze. Although the frequency of occurrence of winters in which fast-ice forms appears to be decreasing at this latitude on the West Antarctic Peninsula (Vaughan et al. 2003), over evolutionary timescales the seasonal variation of disturbance caused by the winter freezing and summer break-up of fast ice is likely to have influenced the evolution of present day life-history strategies. That is, increased disturbance by ice in summer may exert a selective pressure towards winter settlement in sessile taxa.

Further theoretical advantages of winter settlement may be gained in terms of body size, and a trend towards winter settlement may be indicative of adaptations related to optimising growth. Firstly, post-settlement winter growth fuelled by nanophytoplankton production may afford a partial size refuge from predation and

disturbance at the onset of summer. This is particularly relevant for modular organisms which can tolerate substantial colony loss once beyond the ancestrula stage (Greene et al. 1983, Barnes & Arnold 2001a), but the attainment of a size threshold has also been shown to be critical to the survival of solitary ascidians in some environments (Osman & Whitlatch 1998). Secondly, as the utilisable size range of food particles increases with body size in the early development of taxa such as ascidians, post-settlement growth in winter, using the available nanoplankton fraction, may allow them to attain a size at which they are able make more efficient use of the larger phytoplankton elements which bloom in summer (Clarke & Leakey 1996) and thus achieve optimal growth rates through their first year. Thirdly, weakly competitive, ephemeral species may reach reproductive maturity earlier as a consequence of winter settlement and thus be able to release larvae before being overgrown by superior competitors during the summer. If this were the case, a sequence of recruitment periods might be predicted in which there is a progression from poorer to stronger overgrowth competitors from midwinter through to late summer. The recruitment patterns of cheilostome bryozoans observed at a local scale here (Figure 5.5) broadly support this prediction: weaker overgrowth competitors recruiting earlier than stronger competitors. It has previously been suggested that differences in recruitment period may be significant in the persistence of competitively inferior clades over evolutionary timescales (Barnes 2002a) but, to my knowledge, a correlation between recruitment timing and competitive ability at species level has not been demonstrated before.

Many sublittoral colonisation studies have concentrated on recruitment to plate undersurfaces (e.g. Hurlbut 1991a, b, Turner & Todd 1993, Osman & Whitlatch 1995a, Stanwell-Smith & Barnes 1997) with few making comparisons between colonization of upper and lower surfaces (e.g. Nandakumar 1995, Babcock & Mundy 1996, Barnes 1996). The results of the present study, however, show recruitment to upper surfaces which is comparable to, and at times exceeds, that on lower surfaces. This suggests that the observed distributions of established sessile assemblages in this region, in which the protected undersurfaces and overhangs of hard substrata are generally more heavily colonised than are exposed upper surfaces (Barnes 1995c), are the result of post-settlement processes.

The larvae of many benthic species exhibit settlement preferences in response to a variety of environmental cues (e.g. Keough & Downes 1982, Durante 1991, Hurlbut 1993, Rodriguez et al. 1993, McKinney & McKinney 2002, Baird et al. 2003). If larval choice of settlement surface were the principal mechanism controlling distributions in the present study, however, one would not expect to see the significant changes in the ratio of recruitment to upper and lower surfaces observed between seasons (Figure 5.3), and particularly not the seasonal variation observed within individual species such as *Fenestrulina rugula* (Figure 5.8). For these species, if it is assumed that settlement (i.e. the total number of settling larvae) continues to be evenly distributed between upper and lower plate surfaces during the summer months (November to February), as appears to be the case from August to October, the pattern of reduced recruitment to upper surfaces during the summer period suggests that there is increased mortality of recruits on upper surfaces during this period. Other explanations for this pattern might include a change in larval settling behaviour caused by increasing light levels during the onset of summer, but the apparently abrupt decrease in recruitment to upper surfaces in November, rather than a more gradual tailing-off matched to changes in light intensity, argues against this.

Descriptions of non-random distributions caused by post-settlement mortality from predation, grazing, or other biotic disturbances are common in the literature (reviewed in Gosselin & Qian 1997, Hunt & Scheibling 1997). From the evidence in such studies of the effects of grazing by urchins and gastropods, and given the high densities of the urchin *Sterechinus neumayeri* and the limpet *Nacella concinna* in the study area (Chapter 3) and observed grazing on the plates during this study, it seems reasonable to hypothesise that these taxa are responsible for considerable mortality of settling larvae and juveniles on exposed surfaces. Furthermore, Brockington *et al.* (2001) have shown that *Sterechinus neumayeri* is largely inactive during the austral winter but resumes feeding during November, and winter reduction of feeding has also been observed in *N. concinna* (Fraser et al. 2002a, Clarke unpublished data). The correlation of these observations with the decline in upper-surface recruitment observed in November here (Figure 5.8) lends weight to the hypothesis that grazing by these species is reponsible for significant mortality of settling larvae and juveniles of sessile taxa.

Conclusions

In terms of the major taxonomic groups recorded and their relative abundances, the results presented here have many similarities with sessile assemblages recorded in other latitudes (e.g. Greene et al. 1983, Winston & Jackson 1984, Todd & Turner 1986, Holmes et al. 1997, Smith & Witman 1999). The numerical dominance of recruitment by calcareous polychaetes and bryozoans is typical of both temperate and tropical fouling assemblages, as are the high diversity of cheilostome bryozoans and the annual cycles of recruitment suggested here. The effects of benthic grazers and predators on observed distributions are also common to sessile assemblages in other latitudes. However, although, world-wide, there are still few comparable studies of whole-assemblage recruitment at monthly resolution, the feature which most distinguishes the present data from temperate recruitment patterns is the apparent trend for greater numbers of species to recruit during winter. The significance of this trend in terms of life-cycle adaptations to environmental conditions prevailing in the Antarctic over evolutionary time is open to conjecture and, as the present data span only one year, there is clearly a need for longer-term studies to determine the generality of the pattern. It is possible, however, that the life-histories of such species represent adaptation to an environment in which two major agents of disturbance, ice-impact and biological disturbance, peak in the same season as does the availability of food, and thus select for a pattern of winter recruitment. Such a hypothesis is difficult to test but a comparison of the recruitment timings of endemic and non-endemic Antarctic species with overlapping ranges would be a practicable undertaking and would be predicted to show a higher incidence of winter recruitment among endemic species.

Chapter 6 – Assemblage development over 3 years

Chapter 6 - Assemblage development over 3 years

INTRODUCTION

The preceding chapters have shown that benthic assemblages in the study area vary with both depth and location. Assemblages at 8 m are generally less diverse and well-developed than those at 20 m and there can be considerable variability between and within sites at the same depth. For most taxa, however, recruitment does not appear to be a limiting factor at either depth, suggesting that post-settlement factors may be important in structuring assemblages. Ice disturbance is an obvious potential source of mortality, particularly at shallower depths, but the high abundance of vagile taxa at both depths suggests that mortality from grazing and predation may also have an important influence. In this chapter, sessile assemblages at the study sites are monitored through 3 years of continuous development in order to assess post-settlement survivorship and growth.

Existing studies of benthic assemblages in Antarctic nearshore environments suggest three distinctive characteristics. Firstly, growth in most taxa is slow by comparison with similar taxa at lower latitudes (Pearse et al. 1991b, Stanwell-Smith & Barnes 1997, Clarke et al. 2004b). This may be due to physiological limitations associated with low temperature, food limitation due to limited primary production, or a combination of these factors but to date the evidence is not conclusive (Clarke 1991, Hoegh-Guldberg & Pearse 1995, Fraser et al. 2002b, Clarke et al. 2004b). Secondly, growth in many taxa is restricted to the summer period of primary production. Although shell growth in brachiopods and at least one infaunal bivalve species takes place during winter (Peck et al. 1997, Peck et al. 2000), and some bryozoans feed actively throughout the year (Barnes 1995a, Barnes & Clarke 1995), growth in vagile taxa is highly seasonal (Brockington et al. 2001, Fraser et al. 2002a) and for the majority of sessile taxa seasonality of growth has not been measured. Thirdly, the gradient of decreasing physical disturbance by ice with increasing depth is the principal factor determining sessile assemblage structure in nearshore waters (Dayton et al. 1974, Dayton 1990, Barnes et al. 1996, Barnes 1999, Gutt 2001). Again, although the characteristic zonation of nearshore benthic assemblages in the region is probably caused by this gradient, to date only one study has directly linked differences in the

frequency of ice disturbance to differences in assemblage structure (Brown et al. 2004).

Primarily as a consequence of practical difficulties associated with the slow rates of biological processes in the region and loss of equipment through ice impacts during prolonged deployment, only one regularly resurveyed colonisation study has been reported from the Antarctic to date (Stanwell-Smith & Barnes 1997). However, this study was from an arguably unrepresentative location in the maritime Antarctic (Signy Island, 60° 43′ S, 45° 36′ W). The only reports available from continental locations provide very limited information but suggest that growth may not be slow in all taxa (Rauschert 1991) and that recruitment may be highly episodic in some locations (Dayton 1989). In the context of very limited knowledge of colonisation processes in the Antarctic (Dayton 1990, Arntz et al. 1994, Stanwell-Smith & Barnes 1997), the principal aim of the present study was to generate accurate data on the growth, and survivorship of sessile assemblages following intial recruitment. To this end, *in situ* photographic techniques were used to monitor colonisation of artificial hard substrata at each of the study sites used in the earlier chapters. In expectation of slow rates of colonisation and growth (Barnes 1996, Stanwell-Smith & Barnes 1997) the study was designed to span three full annual cycles and to incorporate sufficient replication of locations, and experimental units within locations, to characterise the range of local variability. Beyond these basic requirements, the three assumptions listed above were taken as working hypotheses: 1) growth is slow by comparison with similar assemblages at lower latitudes; 2) growth is highly seasonal and is governed by the summer pulse of primary productivity; 3) differences in the frequency of disturbance by ice are responsible for the observed zonation of sessile assemblages.

METHODS

Study locations & materials

The spatial design of the study and the settlement plate units used are described in detail in Chapter 4. Briefly, arrays of 6 acrylic settlement plates were deployed at each of two depths (~8 m, ~20 m) at each of the three study locations (Hangar Cove, South Cove, Anchorage Island). Assemblages recruiting to both upward and

downward facing surfaces of the plates were monitored at intervals through a 3 year period of continuous immersion.

Sampling

Plates were monitored photographically *in situ* by divers using SCUBA. Photographs were taken on ISO 50 colour reversal film using a Nikonos V 35 mm camera with UW Nikkor 28 mm lens and Nikonos close-up attachment with framer. Lighting was from a Nikon SB105 Speedlight set to TTL metering mode and with diffuser fitted. To illuminate shadow detail, a white plastic reflector (20 cm x 25 cm) was fitted to the leg of the close-up frame.

Settlement plates were deployed at Anchorage and South Cove sites on 13th February 2001, and at Hangar Cove sites on the 22nd February 2001. Diving facilities and records from the first six months of the study were lost in the laboratory fire and, consequently, the first data point was in April 2002, at the end of first year of immersion. From this point, plates were monitored at the beginning of each calendar month until March 2003 (Table 6.1). At each visit, one photograph was taken of each plate surface (upper and lower). Where vagile macrofauna were present on plate upper surfaces, an additional photograph was first taken with these undisturbed and macrofauna were then removed (by gentle fanning) before a second photograph of the upper surface was taken to record the sessile assemblage. Vagile macrofauna other than terebellid polychaetes and nemertean worms on plate undersurfaces were necessarily small, because of the restricted gap (10mm) between plate and base panel, and were left in place.

In March 2003, at the end of the second year of immersion, a set of four overlapping 2:1 macro photographs was taken of the central analysis area (150 mm x 100 mm) of each plate surface to confirm identifications of colonists. In February 2004, at the end of the third year of immersion, all plates from each location were recovered from the seabed and examined under low-power microscopy in the aquarium. At the same time, high-resolution digital photographs were taken of whole assemblages to map colonised areas, and of individual colonists to confirm identifications. At the end of this process, and within one week of retrieval in all cases, all plates were returned to their original sinkers on the seabed. Plates were transported in purpose-built watertight containers and were kept immersed in seawater at ambient temperature at all times to prevent

damage or stress to colonising assemblages. These two detailed examinations (March 2003 and February 2004) ensured accuracy and consistency of identifications but also, importantly, allowed individual colonies to be traced back beyond the point at which their identities could first be resolved from the earlier *in situ* images. By matching the spatial coordinates of an individual, or the ancestrula of a particular colony, in these year-end surveys with corresponding targets in the preceding, lower-resolution images, its history could be followed back to its first appearance on the plates.

Table 6.1 Monitoring dates, total immersion times at each monitoring point (days), and period between successive monitoring points (days) for each location. Nominal month labels (left column) are used in all analyses to simplify presentations. Anchorage sites were inaccessible at the May-02 and Dec-02 monitoring points.

	Hangar			South			Anchorage		
Nominal month	Date	Total	Period	Date	Total	Period	Date	Total	Period
Feb-01	22/02/01	0	-	13/02/01	0	-	13/02/01	0	-
Apr-02	05/04/02	407	407	03/04/02	414	414	07/04/02	418	418
May-02	07/05/02	439	32	09/05/02	450	36			
Jun-02	07/06/02	470	31	10/06/02	482	32	09/06/02	481	63
Jul-02	09/07/02	502	32	11/07/02	513	31	14/07/02	516	35
Aug-02	09/08/02	533	31	12/08/02	545	32	10/08/02	543	27
Sep-02	08/09/02	563	30	11/09/02	575	30	15/09/02	579	36
Oct-02	08/10/02	593	30	10/10/02	604	29	12/10/02	606	27
Nov-02	08/11/02	624	31	10/11/02	635	31	07/11/02	632	26
Dec-02	10/12/02	656	32	12/12/02	667	32			
Jan-03	09/01/03	686	30	10/01/03	696	29	07/01/03	693	61
Feb-03	05/02/03	713	27	06/02/03	723	27	04/02/03	721	28
Mar-03	04/03/03	740	27	05/03/03	750	27	03/03/03	748	27
Feb-04	11/02/04	1084		09/02/04	1091		06/02/04	1088	

Image analysis

Transparencies of whole plate surfaces were scanned (Nikon LS 2000) at a resolution of 600 dpi. The digital images were then cropped to the central 150 cm^2 analysis area registration marks, corrected for minor parallax distortions, and resized to allow global measurement calibration. Image analysis followed the "interactive colour segmentation" method described by Bernhardt and Griffing (2001) using *Adobe Photoshop 7* (Adobe Systems Inc., San Jose, CA) and image analysis routines in *Fovea Pro 3* (Reindeer Graphics Inc., Asheville, NC). Colonies and individuals were

segmented on the basis of their projected area visible in the image. Thus, where overgrowth occurred and where there was significant 3-dimensional structure (which was rare) only the area covered by the uppermost colony or individual was recorded. The fully segmented images enabled areal coverage of each taxon, together with a comprehensive range of positional and form-factor parameters, to be measured automatically using *Fovea Pro 3*.

Growth measurement

Whole-assemblage growth was recorded as change in total percentage area of the substratum covered at successive sampling points. Initial comparisons were made between total areal coverage at the 3 successive year-end points of the study (April 2002, March 2003, February 2004). These allowed annual rates of increase to be compared between locations, depths and years. These rates were then considered in light of seasonal changes in total colonised area measured at monthly increments through the second year of the study (April 2002 – March 2003).

Area measurements of any taxon over the entire analysis area combine all recruits, regardless of their disturbance history, and thus integrate growth, recruitment, and mortality. However, for some taxa, by measuring only individuals or colonies which were unaffected by predation, spatial competition or other disturbance over the observation period, it was possible to measure growth independently. For these measurements of taxon-specific growth, areal coverage of individual specimens was measured at successive monthly sampling points through the second year of the study. Using increase in area as a measure of growth is accurate for 2-dimensional bryozoan forms but is a simplification for the polychaete and ascidian taxa in which there is significant 3-dimensional growth. However, vertical and lateral growth in these taxa evidently occurs simultaneously and measurement of changes in areal coverage therefore still serves to highlight seasonal changes in growth rates.

Although the growth form of encrusting cheilostome bryozoans is simple, at least in early colony development, there is no consensus in the literature as to how growth rates are best compared across taxa and between studies. Growth is most frequently presented as increase in area or number of zooids (e.g. Vail & Wass 1981, Hunter & Hughes 1993, Barnes & Clarke 1998, Barnes & Arnold 2001b) but increase in maximum radius (O'Dea & Okamura 1999), and a specific growth rate index based on

an exponential growth model (Hermansen et al. 2001) have also been used. Here, growth data derived by all three metrics are presented to allow comparisons across a wider range of studies in the literature. Radial growth (d^{-1}) was calculated for each monthly period as:

$$\frac{\left(\frac{D_{eq1} - D_{eq0}}{2}\right)}{t} \qquad \text{Equation 6.1}$$

where D_{eq1} is the diameter of a circle enclosing the same area as the measured colony (equivalent diameter) at the end of the growth period, D_{eq0} is the equivalent diameter at the start of the growth period and t is the growth period in days. Using this metric instead of direct measurement of radius facilitated the automation of measurement and avoided errors associated with reliably determining the colony centre in successive images. The specific growth rate for each monthly growth increment was calculated from equation (3) in Hermansen et al (2001):

$$\mu = \frac{\ln\left(\frac{N}{N_0}\right)}{t} \qquad \text{Equation 6.2}$$

where N is colony area at the end of the growth period, N_0 is area at the start of the growth period, t is the growth period in days, and μ is the specific growth rate.

Growth in circular, unilaminar, colonies of modular organisms is constrained to a quadratic growth function (Hughes 1989) and the majority of encrusting bryozoan colonies in the present study retained this shape throughout the three years. Therefore, the growth model used by Hermansen et al. (2001) might be questionable in this application. However, this metric affords the best opportunities for comparison with existing studies and the simultaneous use of radial growth measurements here provides a reference to ensure that no obviously erroneous values occur.

Comparisons with surrounding assemblages

Assemblages on the experimental substrata after 1 yr, 2 yr, and 3 yr immersion were compared with those identified in photoquadrat surveys of natural substrata surrounding the study sites and on rocks recovered from the seabed at these sites (Chapter 3). Further comparison was made with taxa recruiting to short-term

immersion settlement plates deployed at monthly intervals through the second year of the study (Chapter 5).

Nine classes of sessile fauna were recorded on both natural and artificial substrata but the level of taxonomic resolution below this level was variable both within and between data sets depending on taxon and stage of development. Thus, whereas cheilostome bryozoans were identifiable to species level in all data sets, adult sponges and ascidians were more readily identified on natural substrata than were new recruits and juveniles on plates. Therefore, initial comparisons were based on simple counts of the numbers of individual taxa recorded in each of the 9 principal classes of sessile fauna present across the 3 data sets. Where species, genus or family identifications were consistent across data sets, the presence or absence of individual taxa in each data set was also compared.

Approximate rates of convergence with assemblages on natural substrata at each study site were estimated by means of multivariate analysis methods using the PRIMER statistical package (PRIMER-e Ltd., Plymouth, UK). These analyses employ both taxonomic and quantitative data and thus yield a more comprehensive picture than the initial qualitative comparisons above. Areal coverage and taxonomic data for surrounding assemblages were taken from photoquadrats (150 cm^2) of exposed natural substrata and from rocks collected from the study sites (Chapter 3). Assemblages on plate upper surfaces were compared with assemblages in the photoquadrats, and assemblages on plate upper and lower surfaces combined were compared with assemblages on the collected rocks. In order to allow direct comparisons, differences in the levels of taxonomic resolution between data sets were removed by aggregating to higher taxonomic levels where necessary. For instance, bryozoans could not be resolved to species level in the photoquadrats. Therefore, for all comparisons involving photoquadrat data, bryozoans were grouped as either encrusting or erect species. Comparisons were conducted separately for each site (i.e. depth × location) and were based on matrices of Bray-Curtis similarities calculated from square root-transformed data. By using a relatively mild transformation, relationships between abundances were conserved while preventing similarity values from being driven entirely by the most abundant spatial dominants.

The ANOSIM *R* statistic was used to quantify variations in overall similarity between assemblages. ANOSIM is a permutation-based significance test for multivariate data, which compares rank similarities between samples from different groups in the matrix of Bray-Curtis similarities (Clarke & Warwick 2001). The *R* statistic ranges between +1 and –1 and can be used as a direct comparative measure of the degree of separation between groups of samples (Philippi et al. 1998, Clarke & Warwick 2001, Conlan & Kvitek 2005). Values closer to zero indicate greater similarity between sample groups and a value of 1 indicates complete dissimilarity, i.e. all replicates in one group are more similar to each other than they are to any samples in other groups. Negative values occur when similarities between samples in different groups are greater than similarities between replicates within one or both groups in the comparison.

RESULTS

Ice damage

During the three-year immersion period a total of 9 units were damaged by ice impact: all of these were at 8 m sites (Table 6.2). One unit at the 20 m site in South Cove was also damaged by a rock-fall presumably caused by ice impact above the site. In each case, a new plate was installed and monitoring continued as before. These plates were considered to represent patches of natural substratum from which all sessile taxa have been removed by ice scour and on which assemblage development begins again from first colonisation. At each of the 8 m sites ice damage occurred only once during the three years of the study.

Taxonomic diversity

A total of 32 sessile faunal taxa from 6 phyla, together with one coralline alga, were recorded within the central analysis areas of the plates (Table 6.3). Cheilostome bryozoans were readily identified from photographs, usually to species level. Other taxa could generally be differentiated consistently on the basis of appearance but many could not be identified to species without removal from the plates and consequent disturbance of the assemblage. Thus, 3 types of sponge (distinguished only by colour), 4 types (genera) of cyclostome bryozoan, 2 types (1 genus, 1 species) of solitary ascidian, and 2 types (1 genus, 1 indeterminate) of hydrozoan were recorded, while spirorbid and serpulid polychaete groups each potentially contain more than one

species. Despite these differences in taxonomic resolution, cheilostome bryozoans were evidently the most speciose group and together with spirorbid polychaetes were the most abundant group both in terms of numbers of recruits and areal coverage.

Table 6.2 Settlement plate units replaced following damage by ice impact between February 2001 and February 2004.

		Date replaced	
Location	**Unit**	**8m**	**20m**
South Cove	3	06 Apr 2001	
	1	05 May 2001	
	5	05 May 2001	05 May 2001
	6	05 May 2001	
Hangar Cove	1	11 Apr 2002	
	2	11 Apr 2002	
	4	11 Apr 2002	
Anchorage	6	07 Apr 2002	
	5	14 Jul 2002	

At all locations, at both depths, and throughout the immersion period, there were more taxa present on plate lower-surfaces than on upper-surfaces. At 8m sites, only coralline algae and spirorbid polychaetes survived on upper surfaces, whereas at 20 m a total of 12 taxa were recorded on upper surfaces, including serpulid polychaetes, several species of cheilostome bryozoan, one hydroid, and two specimens of the octocoral *Primnoella antarctica*. However, these taxa occurred in low numbers as isolated individuals or colonies and spirorbid polychaetes and coralline algae were again the most widespread and abundant taxa. The maximum number of taxa on the upper surface of a single plate was 8, recorded from August to November 2002 at the Anchorage 20m site, but by February 2004 this number had been reduced to 3. Except where specified otherwise, the following results refer only to assemblages on the lower surfaces of plates.

Following initial colonisation during the first year of immersion, the mean number of taxa (Figure 6.1) varied little at all sites except 20 m at Anchorage, where numbers were the same as at South Cove after 1 yr, but declined through the second year and remained low after 3 yr. The total number of taxa at both depths in Hangar Cove and at 20 m in South Cove increased slowly to between 14 and 18 after 3 yr, but at 8 m in South Cove and both depths at Anchorage, total numbers remained static or declined. From successive images of assemblages at each site, it was clear that there was little

turnover of species underlying these patterns and in most cases the final assemblage after 3 yr (Table 6.3) consisted largely of the same taxa that had colonised in the first year of immersion. Only at the Hangar Cove 8 m site were the numbers of new taxa recruiting similar in each year of the study; at all other sites the majority of taxa recruited during the first year (Figure 6.2). Indeed, on the undersurfaces of plates where there was little or no disturbance (primarily South Cove), colonies and individuals which were present at the end of the first year generally persisted throughout the study (Figure 6.3).

Assemblages on lower surfaces at 8 m typically were dominated by spirorbid polychaetes and the cheilostome bryozoans *Fenestrulina rugula* and *Arachnopusia inchoata*. However, Hangar Cove plates differed from those at South Cove and Anchorage, in having substantially lower cover by spirorbids (Table 6.4a). At 20 m sites, these three taxa were again present but there were differences between locations in the areal coverage and taxonomic composition of assemblages (Table 6.4b). In South Cove, assemblages were dominated by *F. rugula, A. inchoata,* and the cheilostome bryozoan *Chaperiopsis protecta*, with spirorbids occupying only ~2 %. At Hangar Cove, plates were similar in taxonomic composition to those at South Cove, but with a higher abundance of serpulid polychaetes. At Anchorage, no taxon survived as more than isolated individuals or colonies during the entire study period.

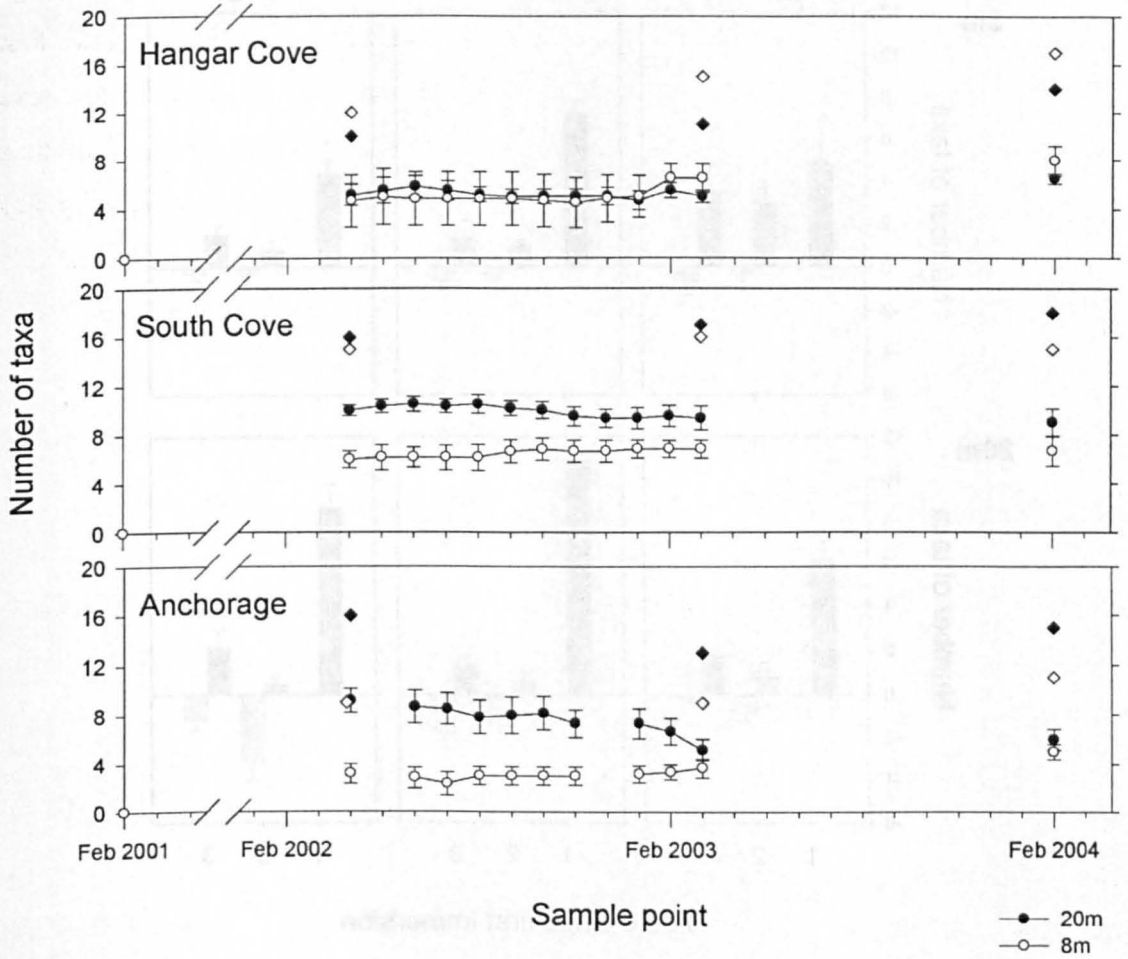


Figure 6.1 Numbers of sessile taxa colonising the lower surfaces of plates immersed for 3 yr at each of 3 locations and 2 depths. Circles show mean number of taxa at each sampling point: filled circles, 20 m sites; open circles, 8 m sites, n = 6 plates, error terms 1SE. Diamonds show the total number of taxa (summed across all plates at each given depth and location) recorded at the end of each year of immersion (April 2002, March 2003, February 2004).

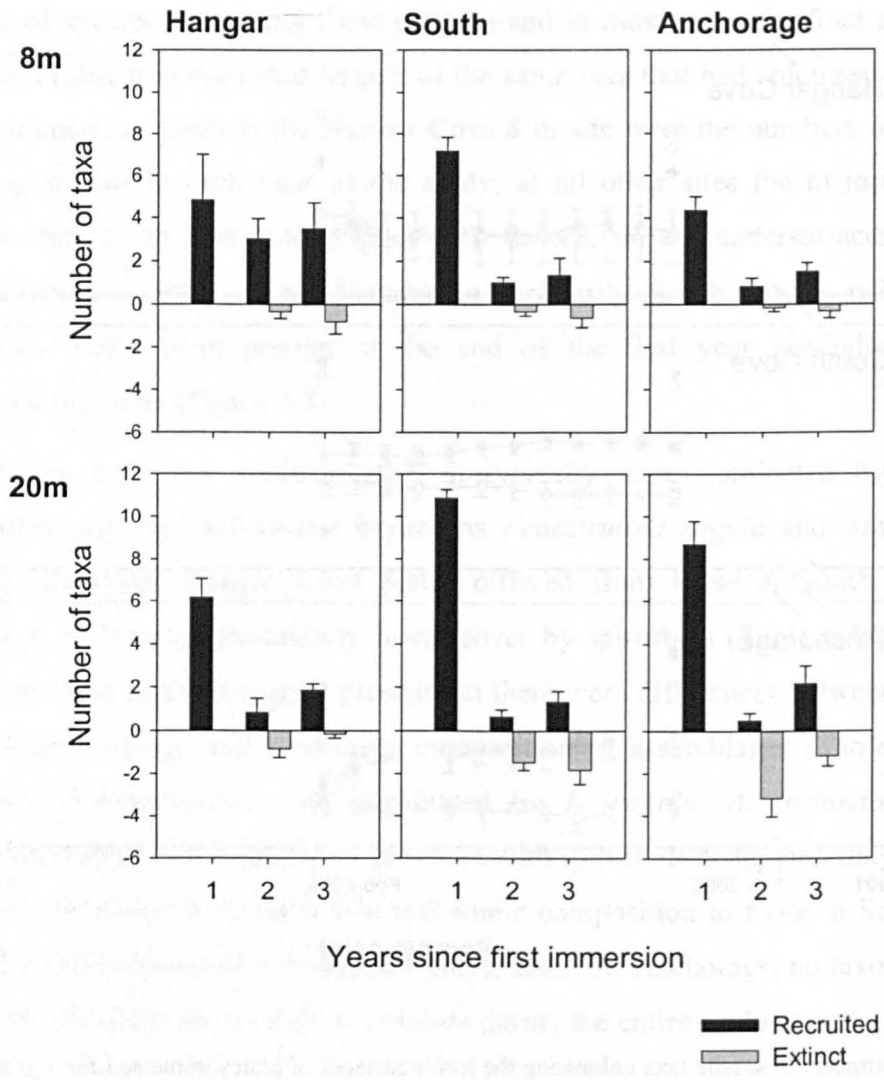
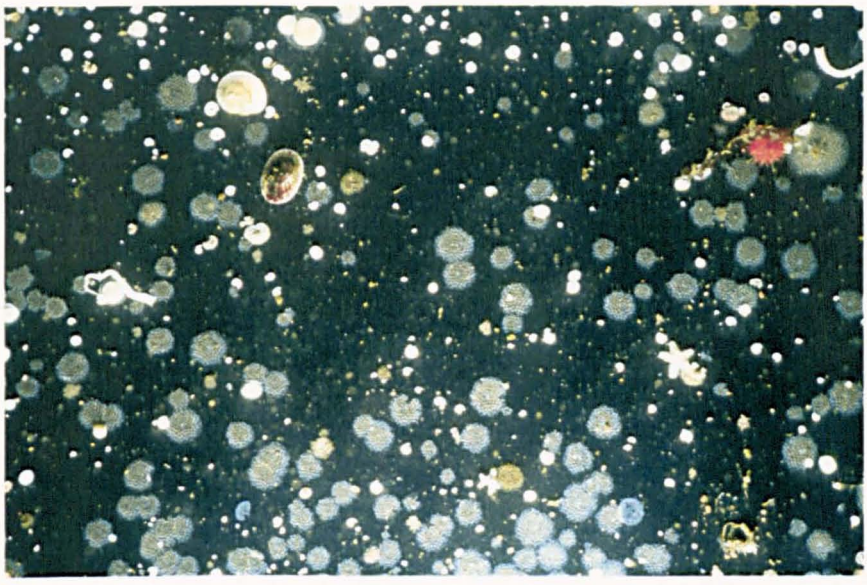


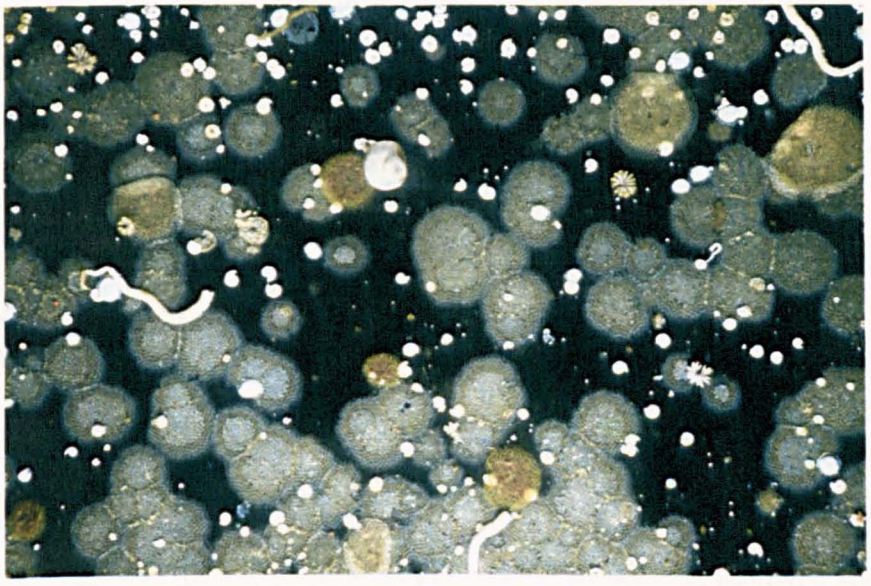
Figure 6.2 Species turnover on continuously immersed plates over 3 yr (upper and lower surfaces, combined area 300 cm^2). Positive bars (black) show the mean number of new species recorded at the end of each year of immersion, negative bars (grey) show the mean number of species lost, n = 6 plates, error terms 1SE. Recruitment in year 1 is significantly greater than in years 2 and 3 (Kruskal-Wallis tests, $P < 0.05$) at all sites except Hangar Cove 8 m, where differences between all years were non-significant.

Figure 6.3 (next page) Photographs of the undersurface of a settlement plate at 20 m depth in South Cove after 1, 2, and 3 yr of continuous immersion. Images are cropped to the central 150mm × 100mm analysis area of the plate. After 3 yr (lower panel) the total cover by sessile fauna was 94 % and 9 taxa were present. This was the second highest coverage of any plate in the study. The maximum number of taxa on a single plate was 13, also at this site.

1yr



2yr



3yr

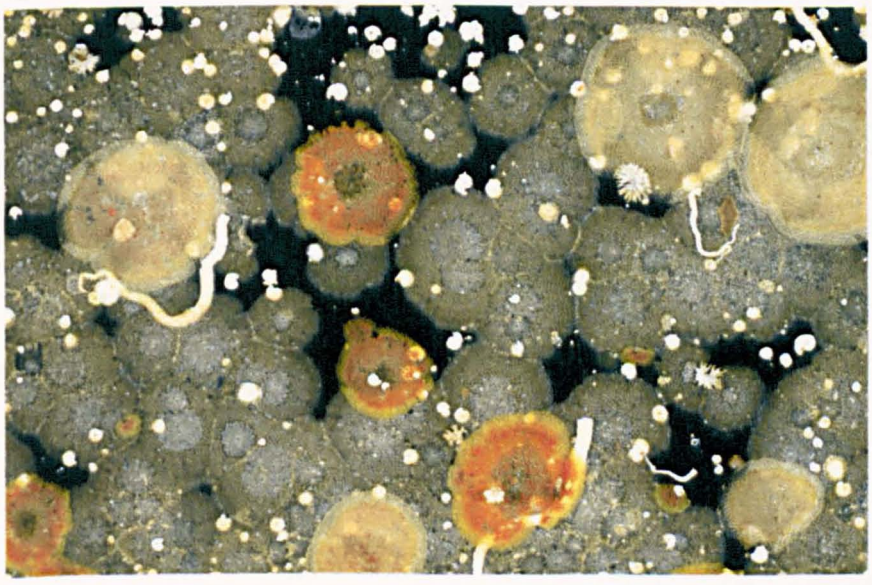


Table 6.3 (this page and facing) Taxa recorded on settlement plates immersed continuously from Feb 2001 to Feb 2004 at 3 locations (Hangar Cove, South Cove, Anchorage) and two depths (8 m, 20 m). Upper and lower surface data are combined and symbols in each column (facing page) indicate presence (•) or absence (○) at 1 yr, 2 yr, and 3 yr monitoring points (1 yr at left).

Phylum	Class	Order	Recorded taxa
Porifera	Demospongiae		Sponge 1 (brown)
			Sponge 2 (white)
			Sponge 3 (orange)
Cnidaria	Hydroida		Stoloniferous hydrozoans
			Tubularia sp.
	Alcyonaceae		*Alcyonium antarcticum*
			Primnoella antarctica
Annelida	Polychaeta	Sabellida	Serpulids
			Spirorbids
Mollusca	Bivalvia		*Adamussium colbecki*
Bryozoa	Stenolaemata	Cyclostomatida	*Lichenopora/Discoporella* spp.
			Tubulipora sp.1
			Tubulipora sp.2
			Idmidronea spp.
	Gymnolaemata	Cheilostomatida	*Aimulosia antarctica*
			Arachnopusia inchoata
			Beania erecta
			Beania costata
			Celleporella antarctica
			Chaperiopsis protecta
			Camptoplites bicornis
			Ellisina antarctica
			Fenestrulina rugula
			Hippadanella inerma
			Lageneschara lyrulata
			Micropora notialis
			Smittina sp.
			Toretocheilum absidatum
			Valdemunitella lata
Chordata	Ascidacea	Phlebobranchia	*Cnemidocarpa verrucosa*
			Ascidia sp.
Algae	Rhodophyta		Coralline encrusting algae

	Hangar Cove		South Cove		Anchorage	
Recorded taxa	8m	20m	8m	20m	8m	20m
Sponge 1 (brown)	●●○	○○●	○○○	○●●	○○○	○○○
Sponge 2 (white)	○○●	○○○	○○○	○○○	○○○	○○○
Sponge 3 (orange)	○○●	○○○	○○○	○○○	○○○	○○○
Stoloniferous hydrozoans	○○●	○○○	○○○	○○○	●○○	●●○
Tubularia sp.	○○○	○○○	○○○	○●●	○○○	○○●
Alcyonium antarcticum	○○○	○○○	●●●	○○○	○○○	○○○
Primnoella antarctica	○○○	○○○	○○○	○○○	○○○	○●●
Serpulids	●●●	●●●	○●●	●●●	●●●	●●●
Spirorbids	●●●	●●●	●●●	●●●	●●●	●●●
Adamussium colbecki	○○○	○○●	○○○	○○○	○○○	○○○
Lichenopora/Discoporella spp.	○○○	●●○	●●○	●●●	●●●	●●●
Tubulipora sp.1	●●●	●●●	●●●	●●●	○○●	●○○
Tubulipora sp.2	○○●	○○○	○○○	●●●	○○○	●○○
Idmidronea spp.	○○○	○○○	○○●	●○○	○○○	●○○
Aimulosia antarctica	○●○	○○○	●●●	●●●	●●●	●●○
Arachnopusia inchoata	●●●	●●●	●●●	●●●	●●●	●●●
Beania erecta	●●●	○○○	●●●	●○●	○●●	●●●
Beania costata	○○○	○○○	○○○	○○○	○○○	●●●
Celleporella antarctica	●●○	○○○	●●●	●●○	○○○	●○●
Chaperiopsis protecta	●●●	●●●	○○○	●●●	○○○	●●●
Camptoplites bicornis	○○●	○○○	○○○	○○●	○○○	○○●
Ellisina antarctica	○●●	○●●	●●●	●●●	●●●	●●●
Fenestrulina rugula	●●●	●●●	●●●	●●●	●●●	●●●
Hippadanella inerma	●●●	○○○	○○○	○○○	○○○	○○○
Lageneschara lyrulata	○●●	●●●	○○○	○○○	○○○	○○○
Micropora notialis	●●●	○○●	●●●	○○○	○○●	○○○
Smittina sp.	○○○	●●●	●●●	●●●	○○○	○○●
Toretocheilum absidatum	○○○	○○○	○○○	○●●	○○○	○○○
Valdemunitella lata	○○○	○○○	●●○	○○○	○○○	○○○
Cnemidocarpa verrucosa	○○○	○○●	○○○	○○○	○○○	○○○
Ascidia sp.	○○○	○○○	●●●	●●●	○○○	○○○
Coralline encrusting algae	●●●	●●●	●●●	●●●	●●●	●●●

Table 6.4 Assemblages on the lower surfaces of acrylic settlement plates at the end of 3 yr continuous immersion (Feb 2001 - Feb 2004) at the three study locations. a) 8 m sites, b) 20 m sites. Taxa within each site are ranked in order of decreasing contribution to overall within-site similarity (SIMPER analysis, 100 % inclusion on fourth-root transformed data). Abundances are given as untransformed mean percentage cover with 1SE in parentheses, n = 6 plates in all cases. Similarity/SD is a relative measure of the consistency of contribution of each taxon to overall within-site similarity; higher values indicate greater consistency.

a) 8 m sites

Location	Taxon	Mean abundance % area (SE)	Sim/SD
Hangar Cove	*Fenestrulina rugula*	35.96 (3.39)	7.59
	Spirorbid polychaetes	1.21 (0.24)	5.68
	Arachnopusia inchoata	3.88 (2.66)	5.09
	Beania erecta	0.18 (0.11)	1.34
	Serpulid polychaetes	0.32 (0.14)	1.19
	Micropora notialis	0.30 (0.13)	0.77
	Tubulipora sp. 1	0.05 (0.04)	0.48
	Camptoplites bicornis	0.03 (0.02)	0.26
	Chaperiopsis protecta	0.05 (0.04)	0.26
South Cove	Spirorbid polychaetes	20.81 (7.78)	4.75
	Fenestrulina rugula	45.70 (10.06)	1.26
	Ellisina antarctica	1.49 (1.06)	1.29
	Arachnopusia inchoata	4.15 (3.02)	0.43
	Tubulipora sp. 1	0.06 (0.04)	0.78
	Serpulid polychaetes	0.22 (0.16)	0.48
	Beania erecta	0.17 (0.10)	0.48
	Aimulosia antarctica	0.06 (0.03)	0.47
	Micropora notialis	0.32 (0.27)	0.26
	Alcyonium antarcticum	0.03 (0.03)	0.26
Anchorage	Spirorbid polychaetes	17.00 (4.99)	5.23
	Fenestrulina rugula	9.85 (4.64)	3.09
	Ellisina antarctica	0.07 (0.02)	1.29
	Serpulid polychaetes	0.13 (0.10)	0.48
	Arachnopusia inchoata	0.72 (0.56)	0.26
	Lichenopora/Discoporella sp.	0.06 (0.04)	0.26
	Aimulosia antarctica	0.19 (0.17)	0.26

Table 6.4 (cont.)

b) 20 m sites

Location	Taxon	Mean abundance (% area (SE))	Sim/SD
Hangar Cove	Spirorbid polychaetes	1.19 (0.47)	6.57
	Serpulid polychaetes	1.45 (0.63)	2.47
	Fenestrulina rugula	7.04 (4.18)	1.24
	Lageneschara lyrulata	0.28 (0.12)	1.16
	Smittina sp.	0.10 (0.05)	0.71
	Tubulipora sp. 1	0.01 (0.01)	0.77
	Arachnopusia inchoata	0.02 (0.01)	0.26
	Sponges	0.02 (0.01)	0.26
South Cove	*Fenestrulina rugula*	54.46 (4.51)	9.06
	Chaperiopsis protecta	6.36 (1.83)	7.46
	Spirorbid polychaetes	1.99 (0.42)	6.37
	Arachnopusia inchoata	4.35 (2.47)	1.34
	Serpulid polychaetes	0.32 (0.22)	0.78
	Smittina sp.	0.20 (0.11)	0.78
	Tubulipora sp. 2	0.08 (0.04)	0.78
	Lichenopora/Discoporella sp.	0.12 (0.08)	0.48
	Tubulipora sp. 1	0.11 (0.08)	0.48
	Aimulosia antarctica	0.03 (0.01)	0.48
	Ascidia sp.	1.65 (1.63)	0.26
	Tubularia sp.	0.02 (0.01)	0.26
Anchorage	*Ellisina antarctica*	0.61 (0.24)	1.24
	Chaperiopsis protecta	0.35 (0.20)	0.72
	Spirorbid polychaetes	0.29 (0.21)	0.76
	Fenestrulina rugula	2.59 (2.52)	0.47
	Beania erecta	0.22 (0.16)	0.48
	Arachnopusia inchoata	1.26 (0.87)	0.26
	Tubularia sp.	0.02 (0.01)	0.26
	Serpulid polychaetes	0.11 (0.09)	0.26

Annual changes in total assemblage cover

On all upper surfaces, throughout the study period, total areal cover was less than 10%, including those plates which were not impacted by ice, and some remained bare after 3 yr (Figure 6.4). Scars where calcareous polychaetes had been removed, presumably by urchin or limpet grazing, were frequently visible on these surfaces and coralline algae were often the only taxa present by the end of the third year.

On lower surfaces at 8 m depth, the maximum rate of increase of total assemblage cover (i.e. growth, mortality, and recruitment combined) was similar across all sites but differences in the timing of ice damage resulted in differences in mean total coverage at all year-end monitoring points (Figure 6.4). At South Cove there was no ice damage after the second month of immersion and assemblages developed at a uniform rate (approximately 25 % of available substratum yr^{-1}) to a mean coverage of 70 % (max. 100 %) after 3 yr. At Hangar Cove, ice damage occurred at the start of the second year but thereafter assemblages continued to develop at the same rate as those in South Cove and after 3 yr mean coverage was the same as that on South Cove plates after 2 yr (40 %). At Anchorage, ice damage occurred at the start of the second year and during the winter of the second year. Here, the mean rate of increase during the first and third years was similar to that at the other locations but there was no net increase in the second year and after 3yr total coverage was not significantly different from that at Hangar Cove (one-way ANOVA $F_{2, 15} = 4.67$, $P = 0.027$, Tukey *post hoc*; South > Hangar = Anchorage).

On lower surfaces at 20 m depth, there were major differences between locations in total areal cover (Figure 6.4). In South Cove, assemblages followed a pattern similar to that seen at 8m, with consistent whole-assemblage growth rates of approximately 25 % of available substratum yr^{-1}. At both Hangar Cove and Anchorage 20 m sites, by contrast, total cover was minimal. At Hangar Cove, at the end of the first year of immersion 20 m plates were similar in areal coverage to those at South Cove. During the winter of the second year of immersion, however, there was a significant decrease in coverage (May – Nov 2002; paired t-test, 5df, $t = 2.39$, $P = 0.03$, evident in Figure 6.5) and total cover remained low throughout the remainder of the study period (average 10%, max. 26% cover after 3 yr). At Anchorage, total cover remained very low throughout the study (average <6 %, max. 19 % cover after 3 yr).

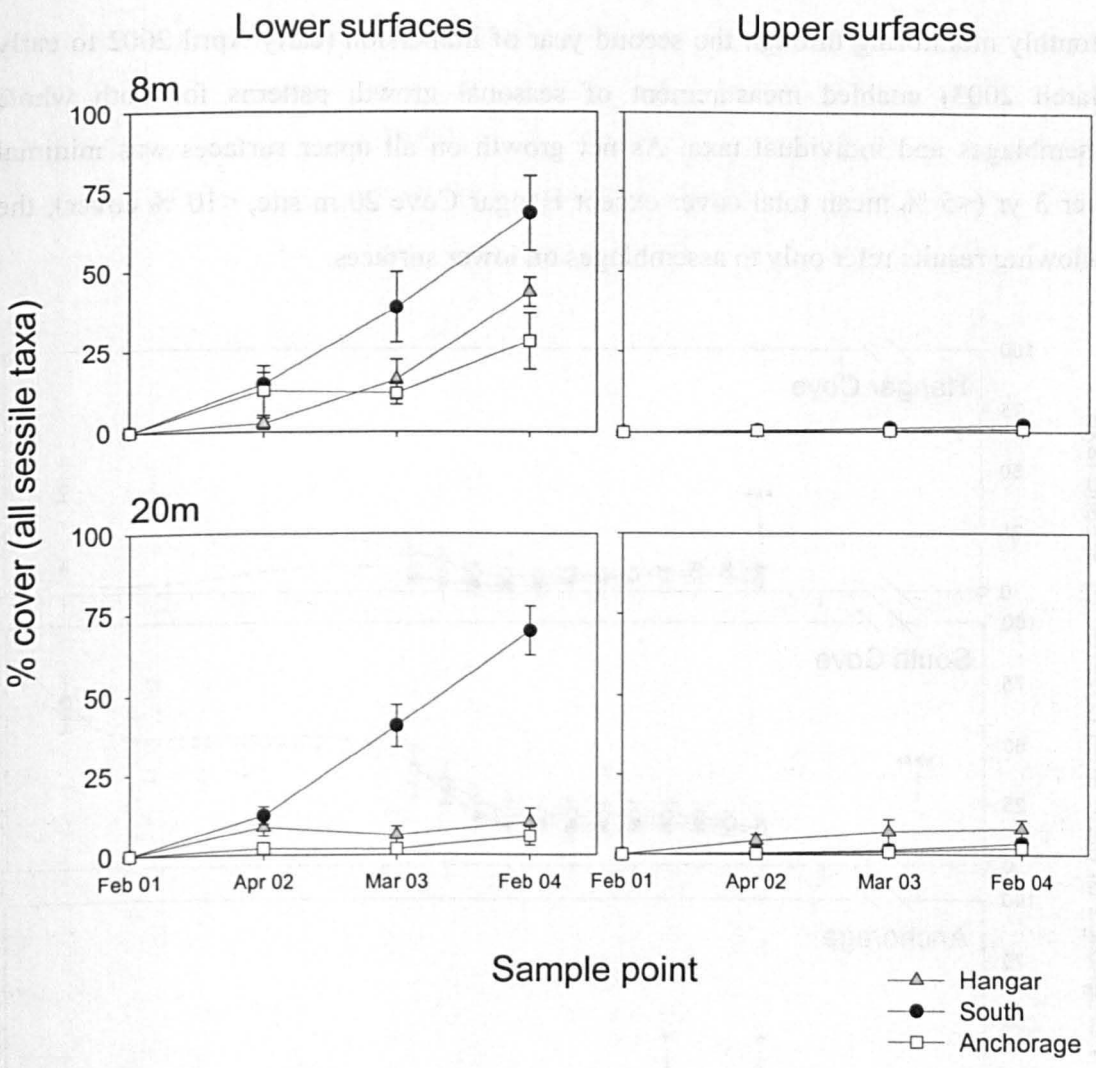


Figure 6.4 Total area (% of substratum) colonised by sessile taxa on upper and lower surfaces of artificial plates after 1, 2, and 3 yr of continuous immersion (immersion period; February 2001 to February 2004). Plates were immersed at two depths (8 m, 20 m) and three locations (Hangar Cove, South Cove, Anchorage). Values are means of n = 6 plates, error terms are 1SE.

Seasonal changes in total assemblage cover

Monthly monitoring through the second year of immersion (early April 2002 to early March 2003) enabled measurement of seasonal growth patterns for both whole assemblages and individual taxa. As net growth on all upper surfaces was minimal over 3 yr (<5 % mean total cover except Hangar Cove 20 m site, <10 % cover), the following results refer only to assemblages on lower surfaces.

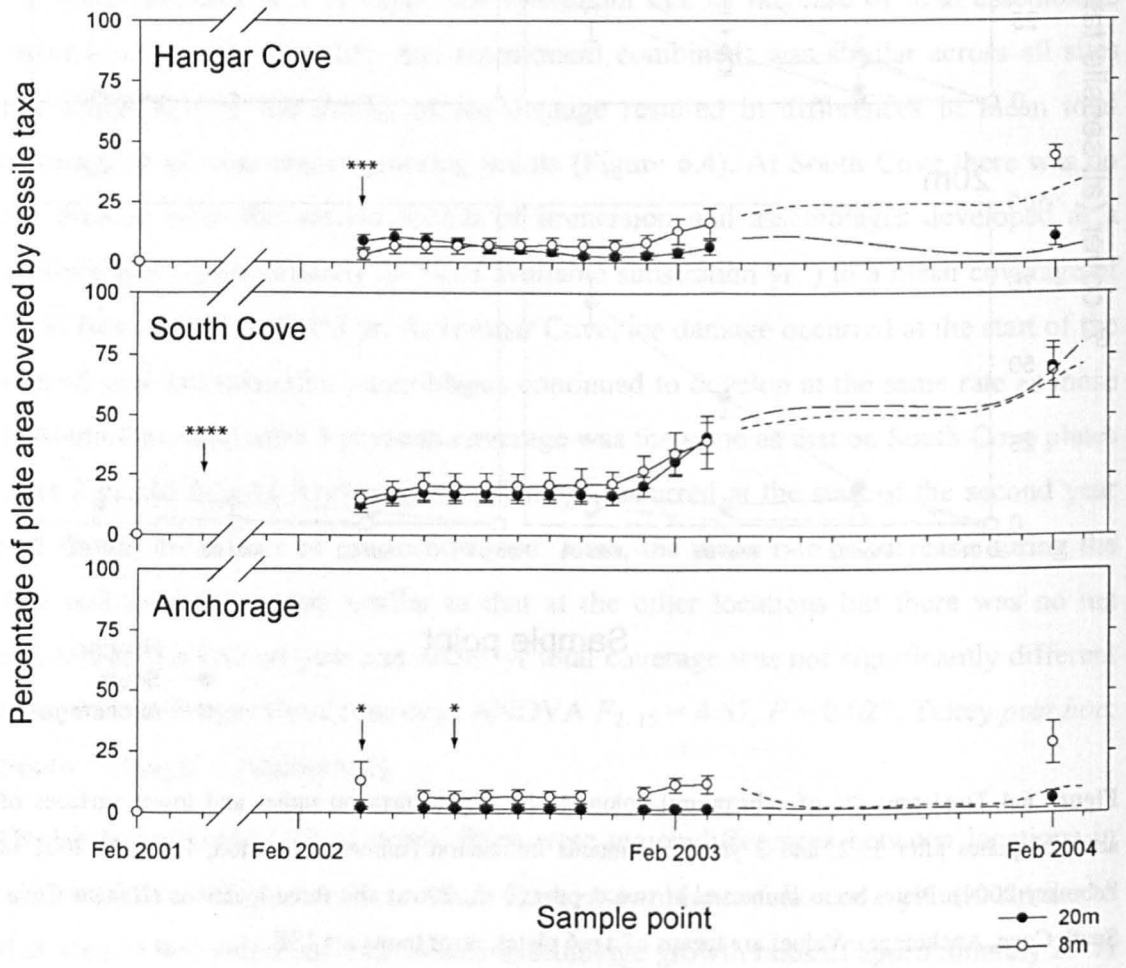


Figure 6.5 Total area of substratum (%) covered by sessile taxa on the lower surfaces of plates (analysed area 150 cm^2) immersed for 3 yr at each of 3 locations and 2 depths. Values are means of n = 6 plates, error terms 1SE. Assemblage development curves recorded at monthly intervals during the second year of immersion (April 2002 – March 2003) are extrapolated through the third year to the final sampling point in February 2004: long dashes, 20 m; short dashes, 8 m. Arrows indicate the timing of ice impacts (at 8 m sites only) and asterisks show the number of plates affected by each impact.

Whole assemblage growth was highly seasonal, with no net growth during the winter from June to November and the greatest increases in areal coverage occurring between January and March (Figure 6.5). This pattern matches changes in the concentration of chlorophyll *a* in the microplanktonic fraction of primary production in the water column during the same period (Figure 6.6). However, the variations in annual growth described above were underlain by pronounced differences in assemblage growth by depth and location at the seasonal level.

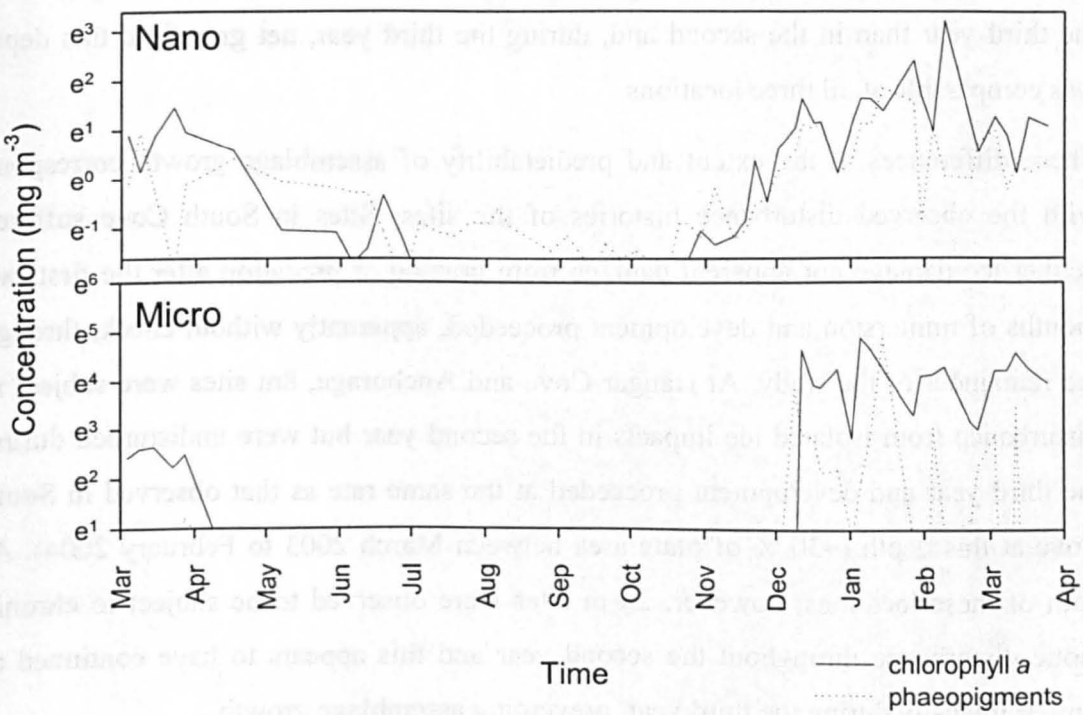


Figure 6.6 Chlorophyll *a* (solid line) and phaeo-pigment (dotted line) concentrations in nanoplankton (2-20 μm, upper panel) and microplankton (>20 μm, lower panel) at 15 m depth in Ryder Bay from March 2002 to April 2003. Data from the Rothera Oceanographic and Biological Time Series (RaTS) project: British Antarctic Survey unpublished data.

To compare overall assemblage development in successive years, curves constructed from mean total coverage measurements at successive monthly intervals during the second year of immersion were extrapolated through to the final monitoring point at the end of the third year (Figure 6.5, broken lines). In South Cove, at both 8 m and 20 m sites, the predicted values for total % cover after 3 yr match closely the observed values at the Feb 2004 monitoring point. At Hangar Cove and Anchorage 20 m sites,

predicted cover after 3 yr is also close to observed values in Feb 2004, but realised assemblage growth remained very low (<15 %) for both of these sites. At Hangar Cove and Anchorage 8 m sites by contrast, realised growth after 3 yr was significantly higher than the values predicted from extrapolation of growth through the second year (t tests, 5df, Hangar Cove $t = 9.66$, $P < 0.001$, Anchorage $t = 3.22$, $P = 0.02$). Thus, at each 20 m site, the net growth of assemblages was consistent from year to year but varied in magnitude between locations and was considerably greater in South Cove than elsewhere. At 8 m sites in Hangar Cove and Anchorage, net growth was greater in the third year than in the second and, during the third year, net growth at this depth was comparable at all three locations.

These differences in the extent and predictability of assemblage growth correspond with the observed disturbance histories of the sites. Sites in South Cove suffered neither ice damage nor apparent damage from grazing or predation after the first two months of immersion and development proceeded, apparently without check, through the remainder of the study. At Hangar Cove and Anchorage, 8m sites were subject to disturbance from isolated ice impacts in the second year but were undisturbed during the third year and development proceeded at the same rate as that observed in South Cove at this depth (~30 % of plate area between March 2003 to February 2004). At both of these locations, however, 20 m sites were observed to be subject to chronic biotic disturbance throughout the second year and this appears to have continued at similar intensity during the third year, preventing assemblage growth.

Growth of individual taxa

Six faunal taxa were suitable for measurement of seasonal growth (i.e. undisturbed specimens were present throughout the second year of immersion): spirorbid polychaetes, serpulid polychaetes, three species of cheilostome bryozoan, and the solitary ascidian *Ascidia* sp. It was also possible to measure growth of coralline algae on two plates at 8 m in South Cove where they apparently escaped grazing and grew consistently through the study. However, individual recruits of coralline algae were too small for reliable measurement of monthly incremental change during the second year and, therefore, only annual growth increments were measured.

Growth was strongly seasonal in bryozoans, and in spirorbid and serpulid polychaetes and corresponded with nanoplankton chlorophyll *a* concentrations (Figure 6.6): most

growth occurring between December and May. For spirorbids and *Ascidia* sp. greatest rates of area increase occurred between December and February but growth was apparently continuous at low rates throughout the winter (Figure 6.7). For the three bryozoan species (Figure 6.8) there was no detectable increase in mean colony area between June and November but both the radial growth and specific growth rate metrics (which factor out the effect of initial colony size and thus reduce variance) indicated that *A. inchoata* colonies may have continued to grow at low rates in all months except September-October. The highest mean rate of radial growth recorded for bryozoans was 0.03 ± 0.001 mm.d^{-1} for *A. inchoata* in the period from February to March, but by the specific growth rate measure, *F. rugula* showed the highest mean growth rate (0.022 ± 0.001 d^{-1} from January to February). Growth of coralline algae was exponential over the 3 years of the study (Figure 6.9) and individual recruits had attained a size of 5.3 ± 0.3 mm^2 after 3 yr. Maximum algal cover on a single plate after 3 yr was 7.8 % at 8 m in South Cove.

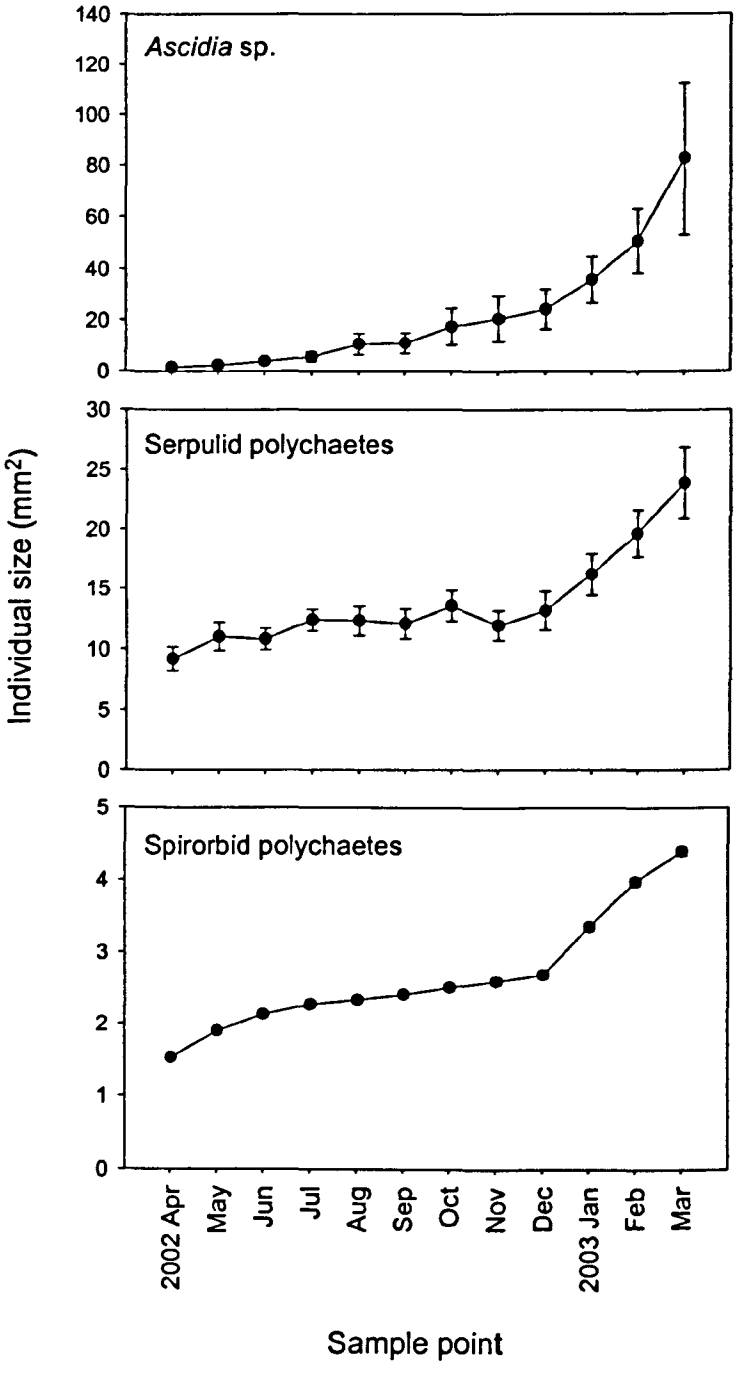


Figure 6.7 *Ascidia* sp., serpulid polychaetes, and spirorbid polychaetes. Growth of undisturbed individuals from April 2002 to March 2003. Values are means of selected individuals across all locations, error bars 1SE. *Ascidia* sp., n = 3; serpulid polychaetes, n = 11; spirorbids, n = 440.

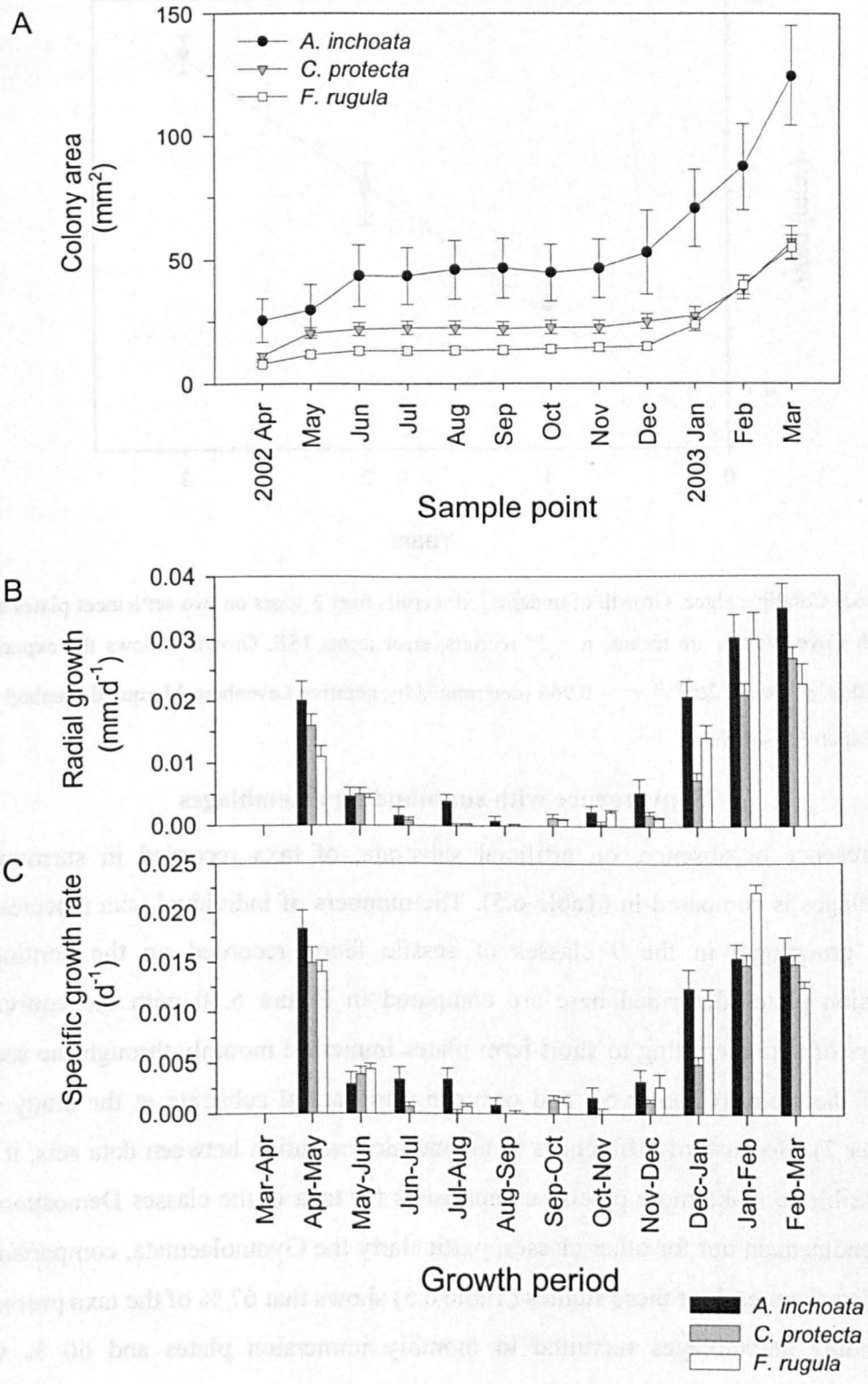


Figure 6.8 *Arachnopusia inchoata, Chaperiopsis protecta, and Fenestrulina rugula*. Growth of undisturbed colonies in free space from April 2002 to March 2003. A; colony area, B; radial growth, C; specific growth rate. Values are means, error terms 1SE. *A. inchoata* n = 10, *C. protecta* n = 20, *F. rugula* n = 50.

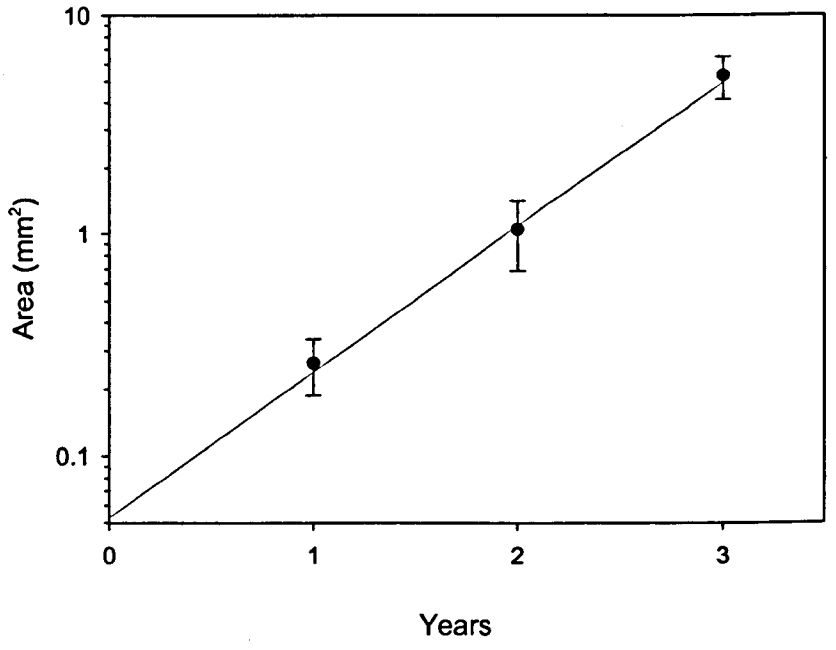


Figure 6.9 Coralline algae. Growth of undamaged recruits over 3 years on two settlement plates at 8 m in South Cove. Values are means, n = 27 recruits, error terms 1SE. Growth follows the exponential relationship: $y = 0.0422e^{1.613x}$, $r^2 = 0.966$ (determined by iterative Levenberg-Marquardt method using Curve Expert 3.2 software).

Convergence with surrounding assemblages

The presence or absence, on artificial substrata, of taxa recorded in surrounding assemblages is compared in (Table 6.5). The numbers of individual taxa (species and higher groupings) in the 9 classes of sessile fauna recorded on the continuous immersion plates described here are compared in Figure 6.10 with the equivalent numbers of taxa recruiting to short-term plates immersed monthly through the second year of the study (Chapter 5), and occurring on natural substrata at the study sites (Chapter 3). Because of differences in taxonomic resolution between data sets, it was not possible to make more precise comparisons for taxa in the classes Demospongiae and Stenolaemata but for other classes, particularly the Gymnolaemata, comparison of taxon lists from each of these studies (Table 6.5) shows that 67 % of the taxa present in surrounding assemblages recruited to monthly immersion plates and 60 % were present on plates immersed for 3 yr. In combination with the presence of similar numbers of taxa in all the major classes at each study site (Figure 6.10), this indicates that assemblages on the plates are broadly representative of hard substratum assemblages in the area. It is notable, however, that ascidians, and to a lesser extent

sponges and anthozoans, rarely recruited successfully to the long-term plates despite frequent and abundant settlement of larvae to short-term plates at all sites (Chapter 5). Indeed, only four ascidian individuals survived on the continuous-immersion plates after 3 yr, and no sponges more than 1 yr old were recorded.

Multivariate analyses using the ANOSIM R statistic to quantify similarity between sessile assemblages on the artificial plates deployed in this study and those on natural substrata indicate considerable differences between convergence rates depending on the type of substratum. Comparisons with assemblages on rocks collected from the study sites (Chapter 3) show different trends for each of the three study locations (Figure 6.11, left panel). At Anchorage, plate assemblages at 8 m were indistinguishable from rock assemblages after one year of immersion ($R \approx 0$), and remained so after three years, whereas assemblages at 20 m converged progressively with rock assemblages over three years in a trend which suggests that assemblages will be indistinguishable after ~4 yr. At South Cove, 8 m plate assemblages were also similar to rock assemblages after 1yr ($R < 0$) but diverged progressively over three years ($R > 0$ at 3 yr) and a similar pattern of divergence was evident for 20m assemblages at South Cove. At Hangar Cove, plate assemblages at both depths remained distinctly different from rock assemblages ($R > 0.4$) with evidence of a slow convergence of 8 m plates.

Comparisons between assemblages on plate upper surfaces and assemblages on exposed natural substrata (Figure 6.11, right panel) indicate slow convergence at 8 m and a more rapid convergence at 20 m at all locations. Rates of convergence appear similar at all locations with the exception of Hangar Cove 20 m plates during the second year of immersion. At 8 m, plate assemblages at Hangar Cove and Anchorage remained distinct from natural substrata after one year ($R \approx 1$) and converged only slowly over the next two years, while South Cove plate assemblages were more similar to natural assemblages in all years but converge at a similar rate. However, for all locations at 8 m, assuming a roughly linear progression, full convergence with surrounding substrata would not be expected to occur in less than ~8 yr. At 20 m, assemblages on the South Cove and Anchorage plates converge steadily with natural assemblages and at all locations, again assuming a linear progression, convergence with natural substrata would take ~5 to 6 yr.

Table 6.5 Presence (■) or absence (□) of sessile taxa: identified on natural substrata at the study sites (Chapter 3); recruiting to plates immersed at monthly intervals from April 2002 – March 2003 (Chapter 5), and on plates immersed continuously for 3 yr (this study). "?" indicates that distinct taxa were present but could not be assigned to species.

Phylum	Class	Taxon	Natural	Monthly	Continuous
Porifera	Demospongiae	sponges	■(7 spp)	■	■ (3 spp)
Cnidaria	Anthozoa	*Alcyonium antarcticum*	■	□	■
		Clavularia frankliniana	■	□	□
		Primnoella sp.	■	■	■
		Urticinopsis antarctica	■	□	□
	Hydrozoa	Hydroids - bush form	■	□	□
		Aglaopheniidae	■	■	■
		Tubullariidae	■	□	■
Annelida	Polychaeta	Sabellidae	■	□	□
		Serpulidae	■	■	■
		Spirorbidae	■	■	■
Mollusca	Bivalvia	*Adamussium colbecki*	■	■	■
Bryozoa	Stenolaemata	Cyclostome bryozoans	■	■	■
	Gymnolaemata	*Aimulosia antarctica*	■	■	■
		Arachnopusia inchoata	■	■	■
		Beania costata	■	□	■
		Beania erecta	■	■	■
		Camptoplites bicornis	■	■	■
		Celleporella antarctica	■	■	■
		Celleporella bougainvillei	■	■	□
		Chaperiopsis protecta	■	■	■
		Ellisina antarctica	■	■	■
		Escaroides tridens	■	□	□
		Fenestrulina exigua	■	□	□
		Fenestrulina rugula	■	■	■
		Figularia discors	■	■	■
		Filaguria spatulata	■	□	□
		Hippadanella inerma	■	■	■
		Lageneschara lyrulata	■	■	■
		Micropora brevissima	■	■	□
		Micropora notialis	■	■	■
		Microporella stenoporta	■	□	□
		Smittina rogickae	■	■	■
		Toretocheilum absidatum	■	□	□
		Valdemunitella lata	■	□	■
		Bryozoans - erect indet.	■	■	□
Brachiopoda	Articulata	*Liothyrella uva antarctica*	■	□	□
Chordata	Ascidacea	*Cnemidocarpa verrucosa*	■	■	■
		Molgula enodis	■	?	□
		Styella wandely	■	?	□
		Pyura discoveryi	■	?	□
		Pyura setosa	■	?	□
		Ascidia sp.	■	■	■

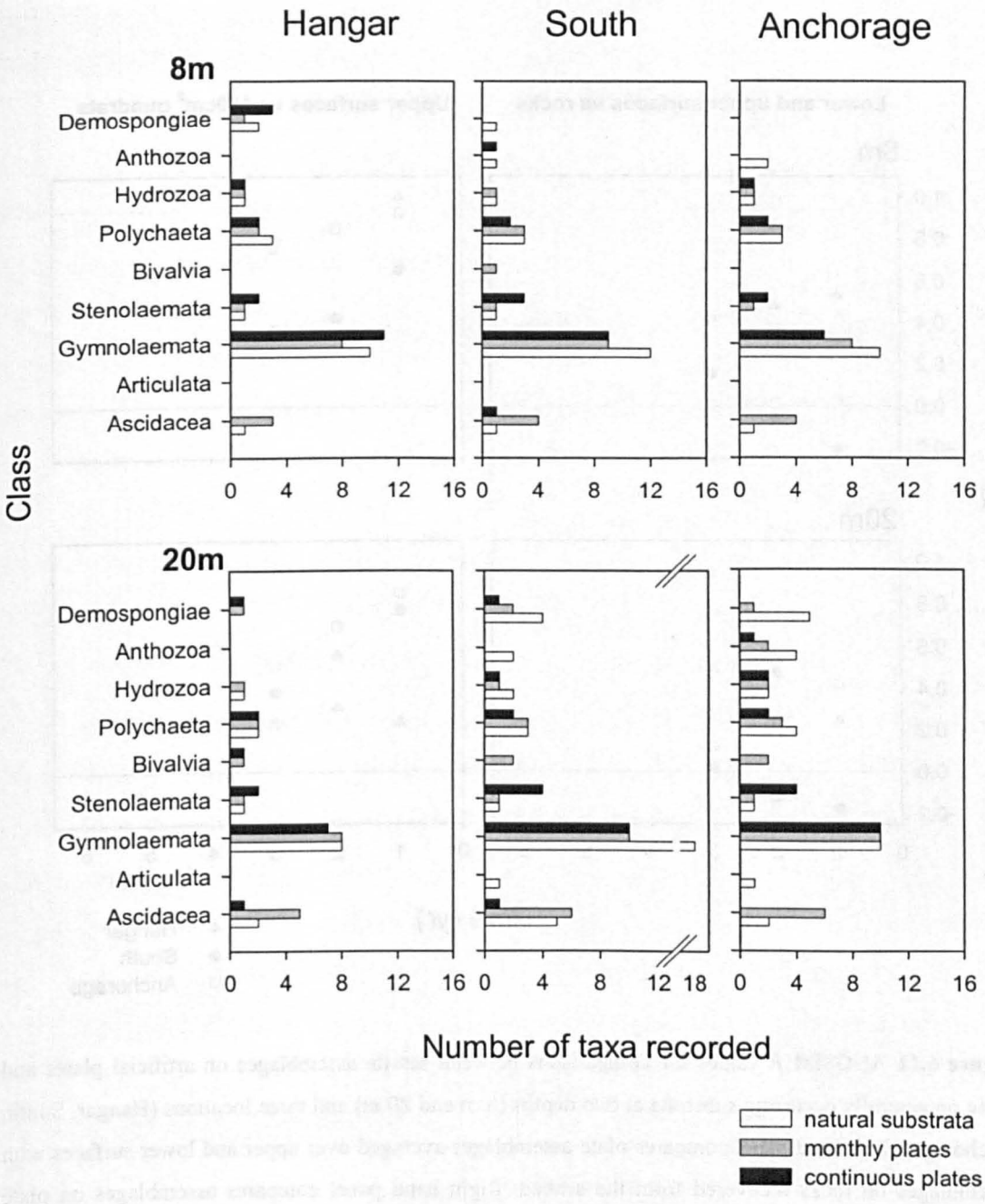


Figure 6.10 Total numbers of taxa (species and other groupings) recorded in the 9 principal classes of sessile taxa. For each depth at each study location, plots compare the number of taxa found on surrounding natural substrata (open bars, data from Chapter 3) and the number recruiting to monthly immersion plates (grey bars, data from Chapter 5), with the number colonising continuously immersed plates after 3 yr (black bars, this study).

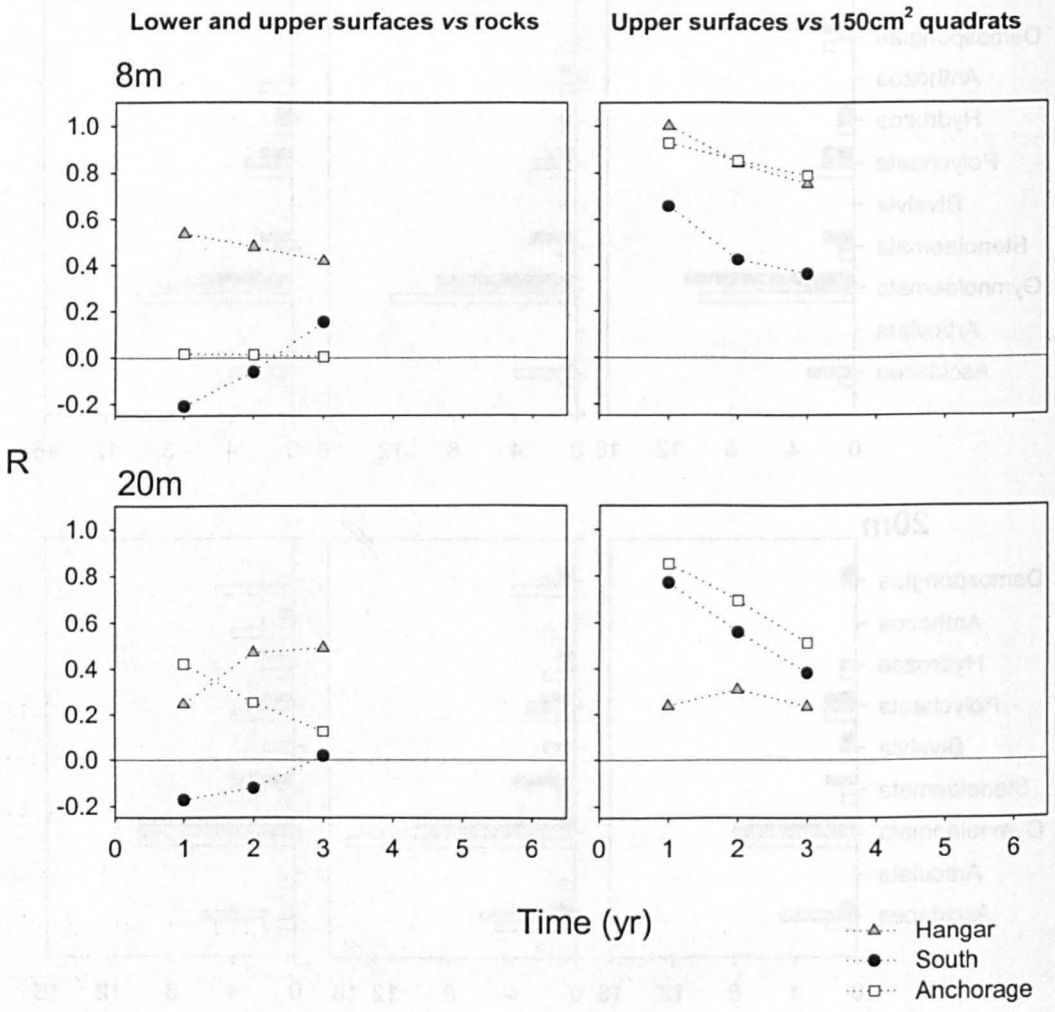


Figure 6.11 ANOSIM *R* values for comparisons between sessile assemblages on artificial plates and those on naturally occurring substrata at two depths (8 m and 20 m) and three locations (Hangar, South, Anchorage). Left hand panel compares plate assemblages averaged over upper and lower surfaces with assemblages on rocks recovered from the seabed. Right hand panel compares assemblages on plate upper surfaces with assemblages recorded in photoquadrats (150 cm^2) of exposed natural substrata. ANOSIM *R* ranges between +1 and –1, values closer to zero indicating greater similarity between comparison groups. Plates, n = 6 in all comparisons; rocks, n = 20; photoquadrats, n = 14.

DISCUSSION

Comparisons with other studies

Despite the theoretical advantages of artificial substrata for making direct comparisons between studies, consideration of data from the present study and a range of published studies (Table 6.7) suggests that such comparisons are not straightforward. Across three locations in the present study, total mean cover on undersurfaces after 3 yr ranged from 6 to 70 % and was qualitatively and quantitatively both highly site-specific and depth-dependent, indicating that colonisation can be heavily influenced by local habitat variability at scales of <5 km. However, many comparable studies report data from only one site, and differences in numbers of replicate plates, depths, and the mode and timing of deployment combine to make even general comparisons problematic. Furthermore, the spatially dominant taxa in one region may be entirely absent from another, leading to potentially meaningless comparisons.

Two points of methodology are particularly important here. Firstly, if plates are suspended above the substratum they may be effectively isolated from benthic grazers and predators and, depending on the distance from the seabed, may not be accessible to sessile taxa with short-dispersal larvae, such as the majority of bryozoans. Assemblage development on such plates may, therefore, be unrepresentative of colonisation processes on the seabed. The heavy growth of solitary ascidians reported by Rauschert (1991) on suspended plates may be an example of this as, unlike most sessile taxa, ascidian eggs and larvae are widely-dispersed in the water-column (Stanwell-Smith et al. 1999, this study chapter 9) and successful recruitment of this taxon appears to be highly susceptible to predation during early development (Sutherland 1974, Osman & Witlach 2005). Similarly, Greene et al. (1983) contrast the dominance by solitary ascidians on their plates in Puget Sound with Jackson's (1977) conclusion that colonial, modular taxa inevitably come to dominate hard substratum fouling assemblages. However, the Puget Sound plates were suspended, and thus isolated from most predation, while Jackson's plates were attached to coral substrata and subject to considerable localised disturbance from fish and urchins (Winston & Jackson 1984).

Secondly, the pronounced seasonality of growth seen for most taxa in the present study results in non-linear growth curves for whole assemblages (Figure 6.5). Therefore, if

plates are deployed in different seasons, or if areal coverage is to be compared in terms of whole years deployed, it is the number of full growth seasons (i.e. summers) encompassed that should be compared rather than the precise number of months. This is of particular importance for comparisons with other Antarctic studies and for all short-term (<1 yr) comparisons. The only detailed colonisation studies from the Antarctic yet published are those of Stanwell-Smith & Barnes (1997) and Barnes (1996) which span 20 and 21 months respectively. However, although the maximum immersion periods of these two studies were very similar, the former encompasses only one summer, while the latter encompasses two, suggesting that they should be considered as 1 yr and 2 yr durations respectively for the purposes of comparison.

Despite these caveats, some broad comparisons can be made. Total percentage cover values from colonisation studies in Antarctic, temperate, and tropical locations are collated in Table 6.7. There are quantitative and qualitative similarities between the two studies conducted at Signy (Barnes 1996, Stanwell-Smith & Barnes 1997) and the present data. Total sessile cover values fall within a common range for each comparable immersion period and the dominant space-occupying taxa were bryozoans and polychaetes. Many bryozoan species were also common to both locations but it is notable that the spatial dominance of assemblages by *Fenestrulina rugula* observed here did not occur at Signy. The other Antarctic study (Rauschert 1991), however, reached a very different end-point after 3 years, with substrata being dominated almost entirely by solitary ascidians. As noted above, this is also the only one of these Antarctic studies in which plates were suspended above the seabed and were thus largely free from predation and disturbance by benthic macrofauna.

Data from the temperate studies indicate a considerably more rapid increase in sessile cover than in the Antarctic, with evidence that assemblages on both suspended and benthic substrata can reach 75 to 100 % cover within 1 year compared with a maximum of 15 % recorded here after 1 year. However, two of these studies used suspended plates and ascidians were again significant occupiers of space and both Osman (1977) and Greene et al. (1983) noted that there was no evidence of predation during their studies. It is also interesting that a large contribution to overall cover in these studies was from barnacles; a taxon which is absent from Antarctic encrusting assemblages. Perhaps more interesting is the variability of areal cover within studies.

For instance, both Osman (1977) and Greene et al. (1983) noted significant declines in areal coverage after initial rapid colonisation and Todd (1998) observed mean coverage which varied depending on season of initial immersion. Many of these fluctuations were associated with rapid colonisation, growth and subsequent decline of a single species within one year and the assemblage dynamics thus differ fundamentally from the persistent species composition and slow growth seen here.

Tropical assemblages also may develop more rapidly than those in the Antarctic but there are few comparable data. In the longest and most detailed of the tropical studies (Winston & Jackson 1984), the dominant taxa on undersurfaces during early colonisation (up to ~1.5 yr) were coralline algae. However, the sponge and bryozoan dominated assemblage which developed later increased at rates which overlap with the range of rates observed for these taxa in the present study (Table 6.7, Figure 6.12). In terms of methodology, replication, mode of deployment, and duration, these data (Winston & Jackson 1984) are the most directly comparable with the present study and none of the obvious confounding factors associated with such comparisons appear to apply. Given the high growth rates reported for some tropical bryozoans (McKinney & Jackson 1989) it seems unlikely that the similarity in rates of increase is a reflection of similarity in unimpeded growth rates. Predation and interspecific competition for both space (Winston & Jackson 1984) and planktonic food (Buss 1979, Buss & Jackson 1981) can be significant in cryptic coral reef assemblages and Winston & Jackson's (1984) data may reflect limitation by these processes rather than slow growth rates *per se*. It would, however, be interesting to compare the total annual availability of planktonic food in persistently oligotrophic tropical waters with that in seasonally highly eutrophic Antarctic waters.

Thus, by the coarse measure of total percentage cover, Antarctic sessile assemblages take in the region of 2.5 to 3 times longer to reach a mean coverage of >50 % than do similar assemblages in temperate latitudes. The realised growth rates of comparable sessile assemblages in the tropics, however, may apparently be similar to those in polar latitudes. The hypothesis of slower colonisation in the Antarctic is, therefore, only partially supported by the rates of assemblage development recorded here.

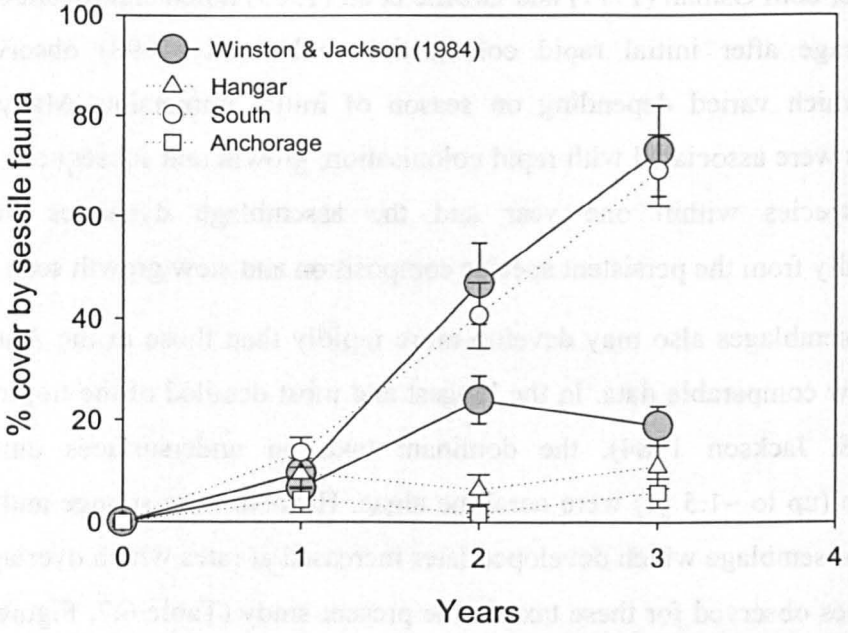


Figure 6.12 Comparison of total % cover by sessile epifauna on the undersurfaces of artificial substrata at 3 sites in the present study (Hangar, South, Anchorage) and 2 sites on a Jamaican coral reef studied by Winston & Jackson (1984). Note that coralline algae have been excluded from the Winston & Jackson data. Present study data are from 20 m, plate area 150 cm^2, n = 6. Winston & Jackson data are from 13 m, plate area 225 cm^2, n = 6.

Growth

Growth was seasonal and coincident with the period of planktonic primary production, thus supporting the second hypothesis. Evidence of continuing growth throughout the year in spirorbid polychaetes, *Ascidia* sp., and *Arachnopusia inchoata* (Figure 6.7, Figure 6.8), however, implies that the ability to exploit limited winter resources, whether from nanoplankton production, resuspension events, or other sources, may be an adaptive advantage. Two of these taxa were conspicuously successful: spirorbids recruited throughout the year at all of the study sites (Chapter 5) and were the most abundant and ubiquitous single taxon in the study, while *A. inchoata* exhibited the highest and most sustained growth rates of all the bryozoans and attained the largest mean colony size. Although only 3 individuals of *Ascidia* sp. survived, this species exhibited the most rapid rates of increase of any taxon. Solitary ascidians are highly vulnerable to predation in the period immediately following settlement (Osman et al. 1992, Osman & Whitlatch 1995b, 1998, 2004) and survivorship of ascidians on plates

in this study was low. It is, therefore, likely that the potential to reach a size refuge from predation through year-round growth is important for the survival of this taxon.

Of the individual taxa for which growth was measured, only the bryozoan species, because of their simplicity of growth form, offer the prospect for realistic comparisons of growth rate with other latitudes. The highest monthly mean specific growth rates recorded here did not differ significantly between the 3 Antarctic bryozoan species but all were significantly lower than rates reported by Hermansen et al (2001) for a range of temperate bryozoan species under varying conditions; median values for the Antarctic species being approximately 5-7 times lower than for the temperate species (Figure 6.13). No suitable data are available to allow calculation of specific growth rates for tropical species, but Winston & Jackson (1984) note that cheilostome growth rates in their study were "generally slow" compared to those reported for temperate species. Perhaps more intuitively useful for the comparison of growth rates is the measurement of radial growth. This measure allows direct comparison of realised growth between colonies of different initial sizes (O'Dea & Okamura 1999) but very few studies provide data from which this rate can be calculated reliably. Values that are available range from 1 $mm.d^{-1}$ (*Conopeum seurati*, O'Dea & Okamura 1999) to 0.3 $mm.d^{-1}$ (*Valdemunitella valdemunita*, Vail & Wass 1981), and these contrast with the highest rate recorded in the present study of 0.03 $mm.d^{-1}$ (*Arachnopusia inchoata*, Feb-Mar 2003). Although such comparisons involve many variables and cannot be conclusive, these figures suggest that even during the period of peak summer growth when food supply is unlikely to be limiting, maximum growth rates of bryozoans in the Antarctic may be at least 10 times slower than those in temperate latitudes.

Taken on their own, the comparisons of growth rates between temperate and Antarctic species lend support to a hypothesis that the low annual growth rates generally observed in Antarctic marine fauna are related to the physiological effects of low temperature *per se* (Hoegh-Guldberg & Pearse 1995, Fraser et al. 2002b) rather than to resource limitation caused by a reduced period of primary production (Clarke 1988, 1991, Clarke et al. 2004b). However, the apparent similarity of realised growth rates between Antarctic species and tropical species of bryozoan suggests an explanation based on food limitation. More comparable data from tropical latitudes are needed to reach any conclusion on this point.

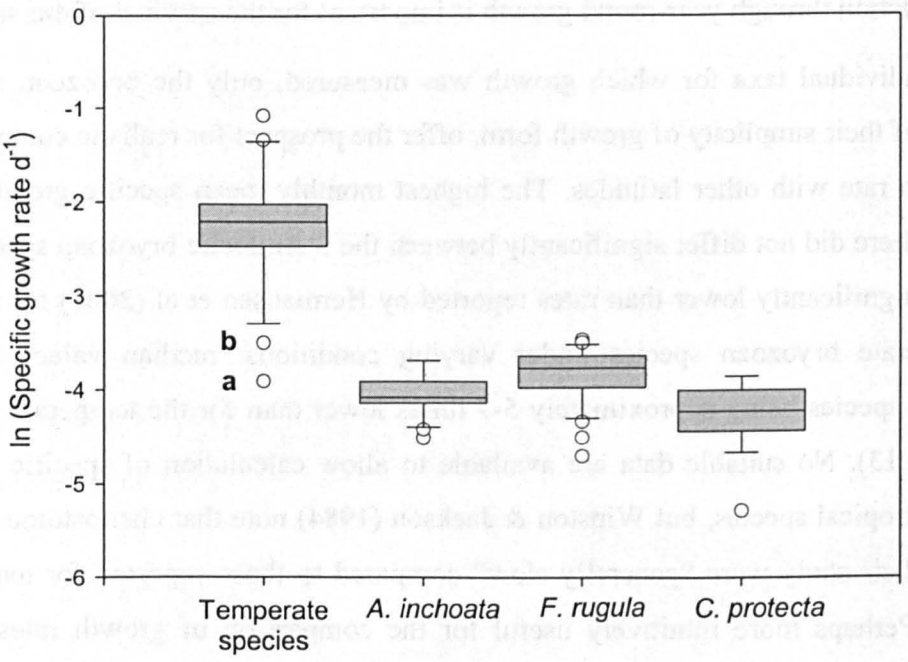


Figure 6.13 Specific growth rates of 3 Antarctic bryozoan species in the present study compared with pooled data for 6 temperate latitude encrusting bryozoan species. Temperate species data are taken directly from Table 7 in Hermansen et al. (2001) and include both field and laboratory studies but exclude erect species. Data from the present study are from unrestricted colonies during months of maximum radial growth for each species: *A. inchoata* and *C. protecta,* Apr-May 2002 and Feb-Mar 2003; *F. rugula*, Jan-Feb 2003. One-way ANOVA on ln-transformed data, $F_{3,92} = 47.9$, $P < 0.0001$, Tukey-Kramer *post hocs*, Temperate species > *A. inchoata* = *F. rugula* = *C. protecta*. (a *Celleporella hyalina*, b *Electra pilosa*: rates are from lowest algal concentrations in laboratory growth studies).

Disturbance

In combination with the abundance and general taxonomic similarity of monthly recruitment recorded at all sites during the study (Chapter 5), the equilibrium in species number over three years here suggests that sessile assemblages in the area are probably not recruitment limited but are controlled largely by post-settlement processes. Disturbance by ice is generally cited as being the principal factor affecting post-settlement survival in Antarctic nearshore waters (Dayton 1990, Arntz et al. 1994, Gutt et al. 1996, Barnes 1999, Gutt 2001, Brown et al. 2004). However, although the depth gradient of ice-mediated disturbance is clearly important, as evidenced here by the relative frequency of impacts at shallow and deep sites, it is not sufficient alone to

explain observed patterns in the present study: few plates were affected by ice and biological disturbances from a range of taxa generally exerted a stronger influence on patterns of colonisation.

The most consistent ecological pattern in this study was the paucity of colonisation on plate upper surfaces and this appears to be primarily a consequence of grazing. Several generalist molluscan grazers (e.g. *Nacella concinna, Iothia coppingeri, Margarella antarctica*) and the urchin *Sterechinus neumayeri* are abundant in the study area (Barnes & Brockington 2003, this study Chapter 3). Grazing and predation by molluscs has been shown to cause significant mortality of early recruits of sessile taxa immediately after settlement in temperate latitudes (Turner & Todd 1991, Osman & Whitlatch 1995b). Grazing by *S. neumayeri,* however, can completely remove bryozoans, spirorbids, and serpulids which have been established for at least one year (This study, Chapter 8) and can also exert a strongly negative effect on early recruitment (Chapter 5). Thus, at the consistently high population densities found in the study area, grazing, particularly by *S. neumayeri,* appears to be a major factor controlling the rate of assemblage development on exposed hard substrata.

The pronounced differences between sessile assemblages on plate undersurfaces across locations at 20 m were also evidently the result of biological disturbances. Undersurfaces were assumed to be protected from most grazing activity by the restricted gap between settlement plate and base panel (10 mm) but a range of generalist grazers (as above), predators (e.g. opisthobranch molluscs, pycnogonids, nemerteans, isopods, errant polychaetes) and crevice-occupying deposit and suspension feeding taxa (terebellid polychaetes, holothurians) affected assemblage development on these surfaces. Although upper surfaces were grazed intensively and uniformly across all study sites at this depth, it is significant that undersurfaces at 20 m were subject to different types and intensities of biotic disturbance at each location. The winter decline in colonised area observed on plates at this depth in Hangar Cove (Figure 6.5) was caused by the grazing activities of small urchins (<10 mm diameter) which were able to move in the gap between plate and base panel (see Chapter 4 for settlement unit design). The very low levels of colonisation observed throughout the study at Anchorage, by contrast, were evidently the result of disturbance by terebellid polychaetes and nemertean worms. Terebellids, in particular, constructed sediment and

gravel tubes in the space between the settlement plate and the base panel. Adult terebellids were surprisingly mobile and it was not uncommon for large adults (up to 150 mm length) to occupy settlement units and construct substantial tubes during the time between monitoring points (~30 d). Once established, however, the majority of these terebellids persisted throughout the study, their tubes occupying large areas of the plate surfaces and thus reducing the free space available to potential recruits of other taxa. At South Cove, although individual bryozoan colonies were occasionally removed by selective predation, possibly by opisthobranch molluscs (Barnes & Bullough 1996), disturbance was minimal.

Disturbances from ice impact and from the activities of macrofauna operated on different temporal and spatial scales and exerted very different effects on the development of sessile assemblages. Ice impacts affected only the sites at 8 m and each impact was an isolated event which did not recur during the course of the study. Significantly, although these impacts were catastrophic for the assemblages affected, not all plates within a site were hit and, across all 8 m sites, 50 % of plates remained unaffected by ice after 3 years. This pattern of disturbance resulted in significant variability in colonisation stage within individual sites but strong similarities between sites across locations. In contrast to this, biotic disturbances evidently continued at the same intensity from one year to the next and affected all plates within the sites where they occurred. For assemblages on lower surfaces, this resulted in a pattern of high similarity between assemblages on plates within each site but significant differences between sites across locations (Table 6.6).

Disturbance by ice, when viewed at smaller scales (cm to m), is an essentially stochastic process: the interacting complexities of seabed topography, iceberg shape, and hydrographical and meteorological conditions combine to render prediction all but impossible other than at the broadest spatial and temporal scales. The intermittent, highly localised, and essentially stochastic nature of ice-mediated disturbance thus permits the existence of both physical and temporal refugia for sessile taxa: the former through the variability of seabed topography, and the latter through the unpredictability of repeat impacts. Disturbance from biotic factors such as grazing, predation, and habitat-modification by macrofauna, by contrast, is the result of targeted behaviour; whether directed at the prey species or at the habitat itself. As such it is likely to persist

for as long as local population densities of the causal macrofauna species remain high and thus is likely to be more predictable at smaller scales. The control of recruitment success by such biological factors has been shown to maintain local assemblage structure in temperate epifaunal habitats over several years (Osman & Whitlatch 1998, 2004) and the consistent differences between the 20 m sites here over 3 years appear to be the result of similar processes.

Table 6.6 Similarity between assemblages on plate undersurfaces at each of the 6 study sites after 3 yr immersion (February 2004 sample point). Values of the ANOSIM *R* statistic are given for pairwise comparisons between the 3 study locations at 8 m and 20 m depths: lower values of R indicate greater similarity. Comparisons are based on a matrix of Bray-Curtis similarities between n = 6 plates at each depth at each location. No transformation of data was used.

	R	
	8m	20m
Hangar Cove *v* South Cove	0.344	0.706
Hangar Cove *v* Anchorage	0.685	0.889
South Cove *v* Anchorage	0.178	0.887

Thus, there are apparently scale-dependent differences in the effects of disturbance which vary according to the causal mechanism: ice disturbance is acute and stochastic, resulting in spatially heterogeneous assemblages at small scales (m) but homogeneity when viewed at larger scales (km), whereas biological disturbance is chronic and targeted and results in homogeneity at small scales and heterogeneity at larger scales. What remains unclear here, however, is why there should be so little biotic disturbance on the undersurfaces of plates at the 20 m site in South Cove when plates at this depth in the other two locations were so heavily affected. Plate upper surfaces in South Cove were affected by grazing as much as were those at other locations and the population densities of terebellid polychaetes and small *S. neumeyeri* in South Cove are similar to those at Anchorage and Hangar Cove respectively (Barnes & Brockington 2003, this study chapter 3), so there is no immediately apparent reason for the absence of disturbance at this site.

Succession and the timing of disturbance

The implications of strongly seasonal growth in the Antarctic extend to considerations of the influence of timing of disturbance on the kind of assemblage that develops. Substrata in temperate studies can develop very different assemblages depending on the timing of first immersion (Sutherland 1974, Todd 1998), indicating that the timing of disturbance, and hence the availability of free space, can be an important factor determining the taxonomic composition of assemblages. This effect is primarily caused by the pre-emption of space by initial recruits which settle in high densities and grow rapidly (e.g. *Ascidia* sp. in Sutherland 1974, *Ascidiella scabra* in Todd 1998); the identity of these initial colonists depending on when the disturbance occurs in relation to species-specific settlement periods (Sutherland 1974). In the Antarctic, however, restricted and strongly seasonal growth may negate the potential for such "lottery" effects (Greene & Schoener 1982) to be generated by variations in the timing of disturbance.

The pre-emption of space requires that growth should occur before other competing taxa recruit to the substratum. However, if most growth takes place within a single short season, none of the recruits which have settled between the end of one growing season and the beginning of the next will have grown significantly and, therefore, all will be at essentially the same size at the start of summer, regardless of when they settled. In the present study, for instance, first immersion during February will have missed the brief summer period of maximum growth and there will have been negligible growth in any taxon during the following 8-9 months up to the beginning of the next summer. Thus, because the competition for space occupation effectively only begins once all competitors are assembled, there is little potential within a single year for any taxon to gain a growth advantage. As competitive overgrowth interactions within high-latitude sessile assemblages are more polarised and deterministic than elsewhere (Barnes 2002b), it also seems probable that the subsequent development of the assemblage will follow a largely predictable course.

In the absence of disturbance, therefore, the combination of slow, temporally restricted growth with consistent recruitment of larvae may result in successional processes during early colonisation being largely deterministic, with the occupation of free space being achieved primarily by high density of recruitment rather than by competitive

interaction or differential growth rates. As free substratum is required for the settlement of most, if not all, the sessile taxa involved, the rapid occupation of space through abundant recruitment, even by competitively inferior species, can have a significant inhibitory effect (*sensu* Connell & Slatyer 1977) on the recruitment of competitors. The stability over 3 years of assemblages dominated by *F. rugula* in South Cove may be an expression of such inhibition. *F. rugula* has limited competitive overgrowth ability (Barnes & Rothery 1996, Barnes & Clarke 1998) but produces large numbers of larvae which recruit within a relatively short period in early summer (Chapter 5), and exhibits maximum growth rates immediately after settlement (Figure 6.8). The combination of high density of settlement and strong initial growth results in the growing margins of individual colonies meeting conspecifics within a relatively short time (1-2 yr) and thus pre-empting settlement by other taxa. Although competitive overgrowth interactions became significant here after 3 years (Figure 6.3), initial rapid space occupation by *F. rugula* significantly reduced the potential for the competitive dominants *A. inchoata* and *C. protecta* to recruit during this time. No instances of intraspecific overgrowth were observed in *F. rugula* and, as most cheilostome bryozoans have short-dispersal, lecithotropic larvae (Jackson 1986, McKinney & Jackson 1989, Todd 1998, Young 2002), it is likely that most colonies on a single plate are genetically related. Thus, by investing in recruitment, a single genotype ("individual") can potentially occupy substratum more rapidly than would be possible by growth alone in an environment where growth rates are low. The conspicuous spatial domination by *F. rugula* in these assemblages (Barnes & Clarke 1998, this study Chapter 3) suggests that this is a successful strategy.

Convergence with assemblages on surrounding substrata

Plate assemblages were indistinguishable from those on rocks within 3 years and often after 1 year of immersion. Convergence with exposed substrata, by contrast would take at least 5 years and probably more by these estimates. The differences between these convergence times probably involve three main factors: the relative stability of substrata; the degree of exposure to biological disturbance, and the growth rates of different taxa. The rocks were necessarily of a size (range; 0.2-5.6 kg) that could be collected by divers and were therefore inherently less stable than the relatively massive plate units (25 kg). Consequently, the average disturbance frequency of rocks is likely

to be higher than that of the plates (Sousa 1979, Barnes et al. 1996) and the convergence times suggest that rocks of this size are disturbed at least once every 3 years and often more frequently. Comparisons with exposed upper surfaces involve the effects of both ice and grazing disturbance and, from the evidence in the rest of the study, it would appear that these factors, rather than slow growth rates *per se,* are the principal cause of the extended convergence times indicated. It is also significant, however, that encrusting coralline algae cover 10-25 % of exposed natural substrata at 20 m, and 50-80 % at 8 m (Chapter 3), and that this taxon is both slow growing and highly resistant to grazing (Dethier & Steneck 2001). From the maximum unrestricted growth rate of coralline algae measured here (Figure 6.9), and assuming continuing exponential growth and the same density of recruitment as found on plates in South Cove, 25 % cover would require at least 4 years, and 80 % cover approximately 5 years, to achieve. This matches estimates from the multivariate analyses and suggests that time to convergence is a function of both post-settlement mortality from grazing and the slow growth rates of those taxa which are most resistant to such grazing. However, it seems likely that the nature of disturbances (both abiotic and biotic) operating across a range of spatial scales and depth-related gradients are such that the seabed will be a patchwork of different successional stages and the concept of assemblage age, therefore, may be something of a meaningless concept unless applied at an extremely localised scale.

Conclusions

These data show colonisation rates and growth of Antarctic sessile encrusting taxa to be slow and, with some exceptions, strongly seasonal. Methodological differences between studies and differences in the taxonomic composition of assemblages, however, render meaningful comparisons with other latitudes problematic and although maximum development rates are evidently slower in the Antarctic than for comparable temperate assemblages, they show unexpected similarities with some tropical cryptic assemblages. Assemblages in the study area appear to be controlled by post-settlement factors rather than recruitment limitation and, at the spatial and temporal scales observed here, biotic disturbances exert a stronger and more consistent influence on assemblage development than does ice impact. These two disturbance mechanisms have different effects on the spatial heterogeneity of assemblages. While

ice disturbance may follow a relatively simple depth-related gradient, biotic disturbance increases with depth but can be highly patchy at intermediate scales (km) and it is likely that observed distributions are the result of complex interactions between these two factors. The combination of slow growth rates and a short growth season may have the effect of reducing assemblage variability caused by differences in the timing of settlement. Such "lottery" effects depend on differential timing of settlement and growth but while there is considerable variability in the timing of settlement in these assemblages (Chapter 5), the reduced period of primary productivity may effectively negate these differences by delaying the onset of growth in early (winter) settlers. The spatial dominant *F. rugula* exhibits a life-history strategy which apparently circumvents this effect by investing in large numbers of short dispersal range larvae. The resulting high recruitment densities result in rapid space pre-emption, despite slow growth rates, through the meeting of neighbouring colonies.

Table 6.7 (next page) data sources:

Todd (1998) from Fig 2

Stanwell-Smith & Barnes (1997) from Fig 4

Barnes (1996) interpolation of min and max values in Table 1

Green et al. (1983) calculated from Fig 2 sites b-g

Osman (1977) from Fig 7 and Table 6

Jackson & Winston (1982) from Table V and p. 144

Winston & Jackson (1984) from Table 1

Holmes et al. (1997) from Table 3 (study excludes soft-bodied taxa)

Table 6.7 Reported values for total percentage cover by sessile taxa on the lower surfaces of artificial hard substrata. Values are means site^{-1}. Where data from more than one site are available, minimum and maximum mean values are shown. Figures in brackets show maximum and minimum % area covered by fauna only (i.e. excluding algae). (* replicate seasonal experiments at one site)

Region	Depth (m)	Plate area (cm^2)	n (sites)	deployment	0.5yr	1yr	1.5yr	2yr	2.5yr	3yr	Dominant taxa	Study
Antarctic	8	150	3	benthic		3-15		12-39		28-68	bryozoans, polychaetes	This study
	20	150	3	benthic		2-12		2-41		6-70	bryozoans, polychaetes	This study
Antarctic	5	100	1	benthic		2					bryozoans, polychaetes	Stanwell-Smith & Barnes (1997)
	25	100	1	benthic		3	11				bryozoans, polychaetes	Stanwell-Smith & Barnes (1997)
Antarctic	12	900	1	benthic				<1			bryozoans, polychaetes	Barnes (1996)
	25	900	1	benthic				~8			bryozoans, polychaetes	Barnes (1996)
Antarctic	30		1	suspended						~100	Ascidians, bryozoans	Rauschert (1991)
Temperate	0.5-2	103	1	suspended	50	78	35	72			bryozoans, ascidians, barnacles	Osman (1977)
Temperate	3	412	5	suspended		85-100		75-90			barnacles, ascidians	Greene, et al. (1983)
Temperate	6-9	175	2	benthic	34-90 (4-45)						coralline algae, bryozoans, polychaetes	Holmes et al. (1997)
Temperate	0.5-1	100	4*	benthic	10-90	45-85	45-80	50-85	65-85	55	bryozoans, sponges, ascidians, barnacles	Todd (1998)
Tropical	10	225	1	benthic			74 (6)				coralline algae	Jackson & Winston (1982)
	22	225	1	benthic			56 (0)				coralline algae	Jackson & Winston (1982)
Tropical	13	225	2	benthic		19-21 (7-9)		58-79 (24-47)		39-81 (19-73)	sponges, bryozoans, algae	Winston & Jackson (1984)
Tropical	6-9	175	2	benthic	47-82 (3-72)						coralline algae, bryozoans, barnacles	Holmes et al. (1997)

Chapter 7 – Recruitment in the immediate sublittoral

Chapter 7 – Recruitment in the immediate sublittoral

INTRODUCTION

Antarctic littoral and shallow sublittoral habitats are subject to high frequencies of ice scour during summer and may freeze completely to depths below chart datum (CD; the level of the lowest astronomical tide) in winter (Barnes 1995b, 1999). Presumably as a consequence of such disturbance, these habitats are predominantly characterised by bare substratum. However, patchy distributions of sessile suspension feeders (primarily bryozoans) may occur on protected undersurfaces, and some vagile invertebrates, particularly amphipods and the limpet *Nacella concinna*, may be locally abundant in summer (Jazdzewski et al. 2001, Kim 2001, Barnes & Brockington 2003),. Although it is intuitively obvious that ice scour is a major cause of post-settlement mortality for benthic taxa on exposed surfaces in shallow polar habitats, there remains a question of whether or not decreased recruitment by comparison with deeper habitats also plays a part in limiting these populations. Such limitation might operate through behavioural adaptations of larvae, such as negative geo- or photo-taxis prior to settlement, or through increased larval mortality caused by physical factors such as reduced salinity in surface waters due to glacial melt water during summer (reviewed by Chia 1974, Pechenik 1999).

In September 2001, following the loss of diving, laboratory, and aquarium facilities, A study of recruitment in the immediate sublittoral was undertaken. The principal aim of the study was to measure the abundance and taxonomic richness of settlement to hard sustrata in the shallowest permanently immersed habitats and to compare this with settlement at the deeper sublittoral sites of the main recruitment study.

METHODS

Study sites

Initially, attempts were made to find suitable sites in South Cove, Hangar Cove, and at Anchorage Island to allow direct comparisons with the main settlement study. However, substrata at Hangar Cove were too unstable and Anchorage was too exposed to the predominant northerly winds for safe working in shallow waters. Therefore, South Cove and three alternative sites were chosen. The resulting design included two

sites on the south coast of Rothera Point and two on the south coast of Lagoon Island (Figure 7.1). Each pair of sites are approximately 500m apart and those at Lagoon are 5km distant from those at Rothera Point. All sites were similar with respect to substratum, being bedrock with scattered boulders and smaller rocks. The Lagoon East site differed from the others, however, in that greater quantities of the brown, frondose alga *Desmarestia antarctica* were present.

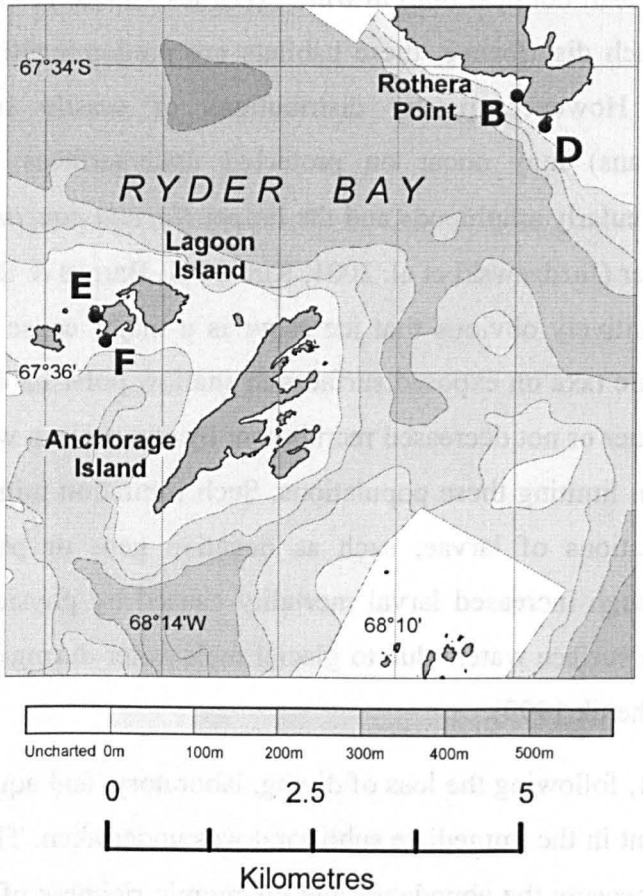


Figure 7.1 Shallow settlement study sites: B, South Cove; D, Cheshire Island; E, Lagoon West; F, Lagoon East.

The study was conducted at depths which could be reached by wading at low water and thus was constained to a maximum depth of ~0.5 m below CD. Actual depths were measured by reference to the tide gauge benchmark on the Rothera wet well, which is set at 5 m above CD. Depths at each study site were determined by simultaneous measurement of water depth at the site (by use of a calibrated 2 m pole), and the vertical distance from water level in the wet well to the tide guage benchmark. Timing of measurements was coordinated by VHF radio.

Settlement plates

Settlement plates were constructed from opaque black acrylic sheet. Plate dimensions were 150 mm x 150 mm overall with a central 100 mm x 100 mm analysis area. The decision to use this size rather than the larger rectangular plates used in the main study was based on three factors. Firstly, they would not be monitored photographically and thus there was no advantage to using the 35 mm photographic frame ratio of the larger plates. Secondly, they would not be attached by the elastic cord system which was devised to allow manipulation while diving. Thirdly, the quantity of acrylic sheet remaining was small and the smaller plate size allowed more plates to be made and thus greater replication. Materials required to construct the sinkers and base plates used in the main study were unavailable, so plates were attached individually to flat rocks collected from the foreshore. Attachment was by means of four 8 mm polyester rope lanyards. One end of each lanyard was passed through a hole drilled though each side of the plate (Figure 7.2) and terminated on the plate undersurface with an overhand knot to prevent it pulling back through. A spliced eye in the other end of the lanyard was passed around to the back of the rock where it was joined to the other three lanyards with nylon cable ties. The overhand knot maintained a gap of ~10 mm between the surface of the rock and the undersurface of the settlement plate, and the cable tie fastenings allowed the plate to be tensioned rigidly to the rock. Lanyards were protected from chafe by sleeves made from plastic hose-pipe.

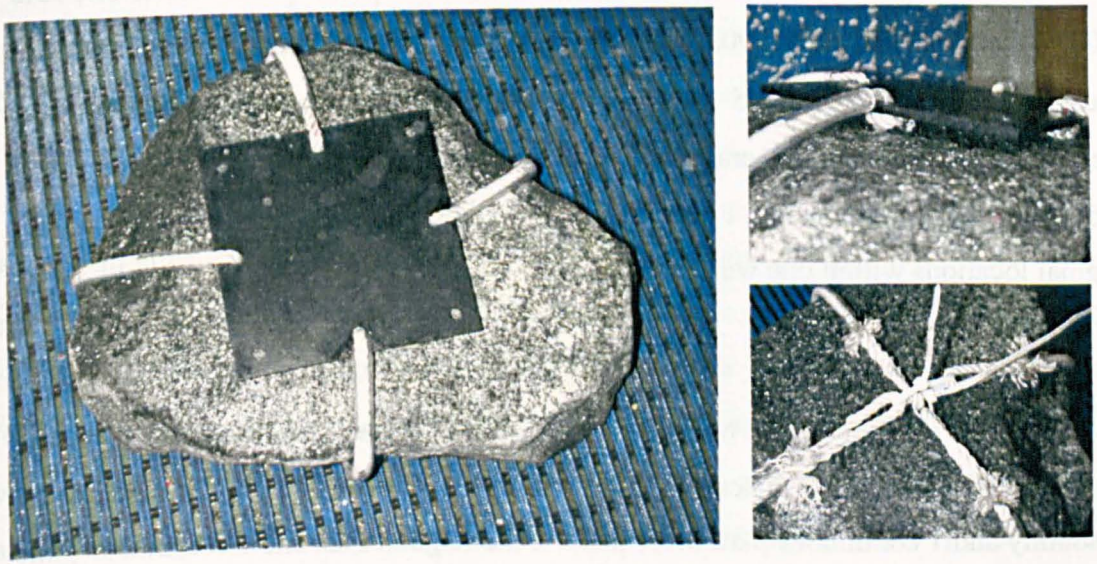


Figure 7.2 Shallow settlement study plate units. Left; plate attached to sinker (viewed from above). Top right; side view showing 10mm gap between plate undersurface and rock. Bottom right; lanyards tensioned by cable ties on undersurface of rock.

A temporary aquarium (0.5 m^3 GRP water tank with Eheim power filter) was set up, initially, in the (unheated) boat shed for the conditioning and storage of settlement plates. Water temperatures in the tank fluctuated with air temperatures, and were elevated by heat from the filter pump, but were <1.5 °C at all times. All plates were immersed on racks in the tank for not less than 7 days before immersion to allow formation of biofilms (see main settlement study methods). In early 2002, a refrigerated transport container was converted for use as an interim aquarium, allowing more precise control of temperatures.

Sampling

At each site, five monthly-replacement and five continuous-immersion plates were deployed at depths of 0.2–0.4 m below CD. Thus, a total of forty units were deployed. Plate units were installed haphazardly but each was placed in a stable position (i.e. between boulders or in angles in the bedrock) to reduce the likelihood of being overturned by wave action.

All plates were deployed between 14^{th}-18^{th} November 2001. Monthly recruitment plates were replaced at approximately 30d intervals (mean immersion period ± 1SE, 29.6 ± 0.5 d). The recovered plates were examined in seawater under low power microscopy and all recruits on both upper and lower plate surfaces were identified to the lowest taxonomic level possible. Continuous immersion plates were examined only twice: in February 2002 after one summer of immersion (mean immersion ± SE, 95.3 ± 0.8 d); and in February 2003 after two summers and one winter of immmersion (mean immersion ± SE, 453.5 ± 1.2 d). On each occasion, the plates were brought back to base, photographed, and all recruits were identified, in the interim aquarium, under low-power microscopy. Following examination, all plates were replaced in their original locations within one week of retrieval.

RESULTS

From the total of 40 plates, 6 were destroyed by ice or wave action during the study. At South Cove, 2 monthly plates and 2 continuous plates were lost. At Cheshire Island, 1 monthly and 1 continuous plate were lost. At the Lagoon East site 1 continuous plate was partially damaged but all other plates at Lagoon remained intact throughout the study. Recruitment of faunal taxa was almost exclusively to the under-surfaces of

plates, with only occasional settlement of hydrozoans, spirorbids and bryozoans recorded on upper surfaces. The following results, therefore, refer only to plate under-surfaces.

Table 7.1 Sessile taxa recruiting to settlement plates at 0.2-0.4 m below CD between November 2001 and February 2003. Symbols indicate presence (●) or absence (○) on plates at each of the study sites. Data are amalgamated from monthly replacement plates (Nov 2001-Jan 2002), and continuous immersion plates (Nov 2001-Feb 2003). Depths below chart datum are shown in brackets below each site name.

			Rothera Point		Lagoon Island	
Phylum	**Class**	**Taxon**	**South** (0.4 m)	**Cheshire** (0.2 m)	**Lagoon E** (0.4 m)	**Lagoon W** (0.2 m)
Rhizopoda		Foraminiferans	○	○	○	●
Cnidaria	Hydroida	Hydrozoans	○	○	●	●
Annelida	Polychaeta	Spirorbid polychaetes	●	●	●	●
Bryozoa	Stenolaemata	*Discoporella* sp. 1	●	○	●	●
		Tubulipora sp. 1	●	○	●	●
		Tubulipora sp. 2			●	●
	Gymnolaemata	*Aimulosia antarctica*	●	●	●	●
		Arachnopusia inchoata	●	○	○	●
		Celleporella antarctica	●	●	●	●
		Celleporella bougainvillei	●	○	●	●
		Celleporella dictyota	●	●	○	●
		Ellisina antarctica	○	●	○	○
		Fenestrulina rugula	●	○	●	●
		Hippandanella inerma	●	●	●	●
		Inversiula nutrix	○	○	○	●
Total number of taxa			10	6	10	14

Taxa

Across all sites and plates (monthly and continuous immersion), a total of 15 sessile invertebrate taxa representing four phyla were recorded (Table 7.1). Highest taxon richness occurred at the Lagoon West site (14 taxa), and the lowest at Cheshire Island (6), the other two sites being intermediate (10 taxa). Mean numbers of taxa per plate were significantly higher at the two Lagoon Island sites than at the Rothera Point sites and, at all sites other than Cheshire Island, the mean number of taxa per plate was significantly lower than the total number of taxa recorded at the site (Figure 7.3). Although these values are influenced by the loss of plates though ice damage at the

two Rothera Point sites, hydrozoans, cyclostome bryozoan type 3, foraminiferans, and the cheilostome brozoan *Inversiula nutrix* were recorded only at Lagoon. Gymnolaemate bryozoans were the most speciose group at all sites, but spirorbid polychaetes were the most abundant.

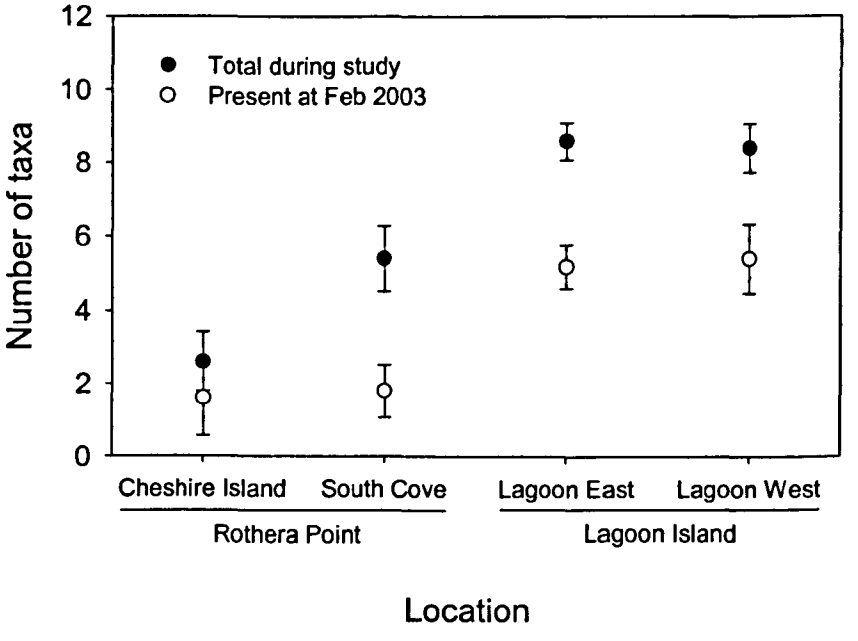


Figure 7.3 Mean number of taxa recorded per plate at each study site. Filled symbols: total recorded over all monthly and continuous plates. Open symbols: number present on continuous-immersion plates in February 2003 after 15 months immersion. Numbers of taxa are significantly lower for sites at Rothera Point than for sites at Lagoon Island (Kruskal-Wallis test, $P < 0.05$). Error terms 1SE. Note that these plots are mean values per plate as opposed to the total numbers of taxa recorded at each site (Table 1).

Recruitment

Short-term recruitment was monitored at monthly intervals from the beginning of the study in November 2001 until February 2002. Recruitment occurred in all three months but the number of recuits per plate was generally very low. The most abundant taxa were spirorbid polychaetes and cyclostome bryozoans and these were rarely present in numbers >20 inds.100cm^{-2}. Mean total recruitment per month, of all taxa combined, did not exceed 20inds.100cm^{2} and was generally <10 inds.100cm^{-2}. On continuous immersion plates, mean total cover by sessile fauna was <1 % at all sites in

February 2002 and <5 % in February 2003 but varied considerably between sites with plates at Cheshire Island remaining uncolonised after 15 months (Figure 7.4, Figure 7.5). Maximum cover on a single plate was 12.4 % at Lagoon East.

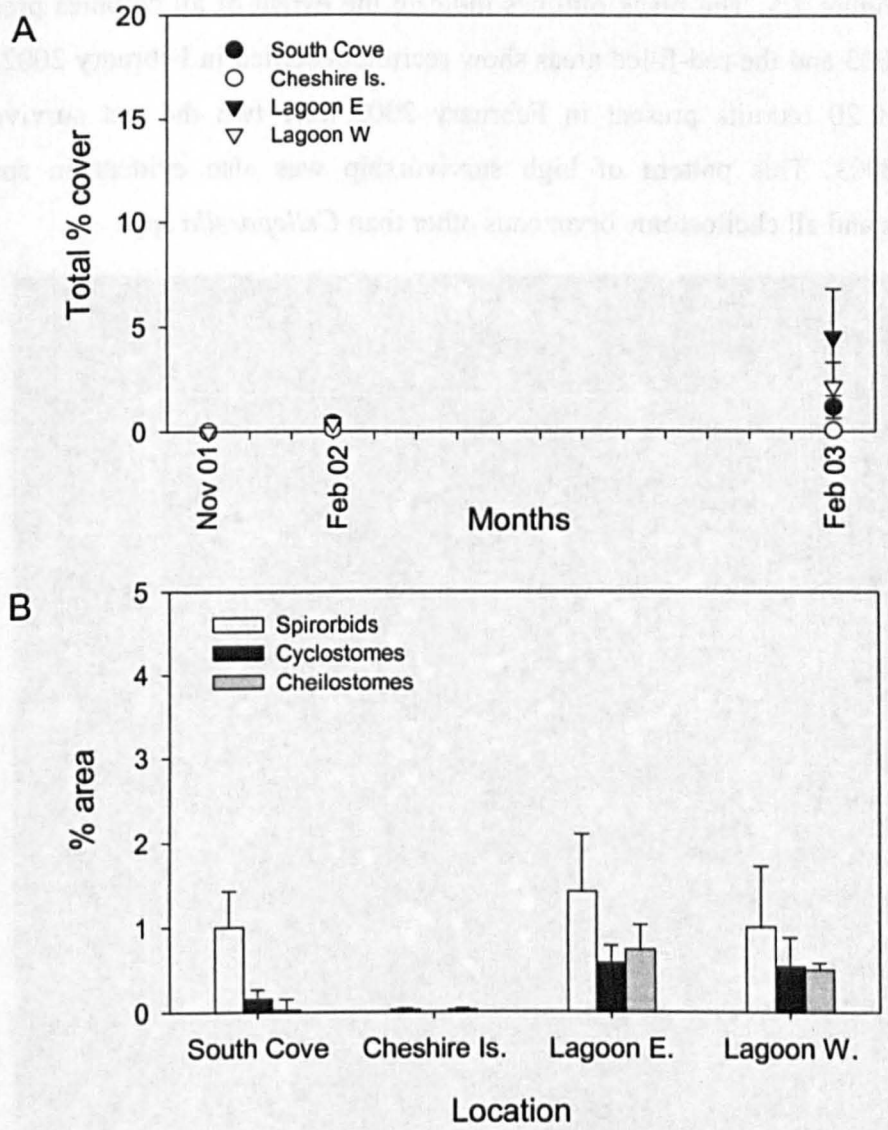


Figure 7.4 Continuous immersion plates. Total % cover by sessile taxa (A) and contribution of the 3 principal sessile groups (B) on undersurfaces of plates immersed continuously from November 2001 to February 2003. Plates destroyed by ice were recorded as having zero cover. n = 5, error terms 1SE.

At the end of these first three months (February 2002), the number and taxonomic composition of recruits on continuously immersed plates was very similar to the summed total of recruitment recorded over this period on the monthly-immersion plates (Figure 7.6), indicating low mortality during this period. Furthermore,

comparison of photographs taken after 3 months and 15 months of immersion showed that the majority of recuits present in February 2002 survived until the following summer and were still present in February 2003. For example, Figure 7.7 shows the distribution of cyclostome (*Tubulipora* sp. 1) colonies on the undersurface of the plate shown in Figure 7.5. The black outlines indicate the extent of all colonies present in February 2003 and the red-filled areas show recruits recorded in February 2002. From the total of 20 recruits present in February 2002 only two did not survive until February 2003. This pattern of high survivorship was also evident in spirorbid polychaetes and all cheilostome bryozoans other than *Celleporella* spp.

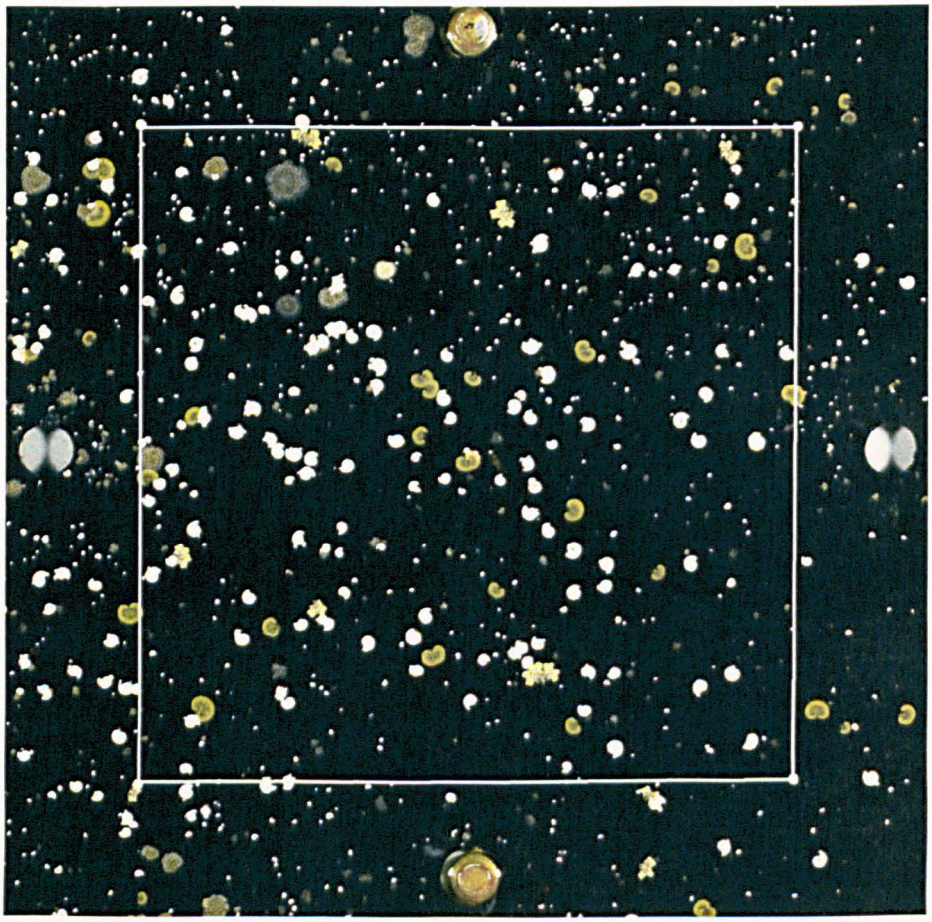


Figure 7.5 Undersurface of a plate immersed continuously for 15 months (17/11/01-12/02/03) at the Lagoon West study site. This plate has the highest number of taxa (8), and the second highest areal coverage (6.7 %) of any in the study. Highest areal coverage (12.4%) occurred on a plate at the Lagoon east site and was caused mainly by high abundance of *Fenestrulina rugula* (7.9% of total coverage). The superimposed white line indicates the 100 cm^2 central analysis area.

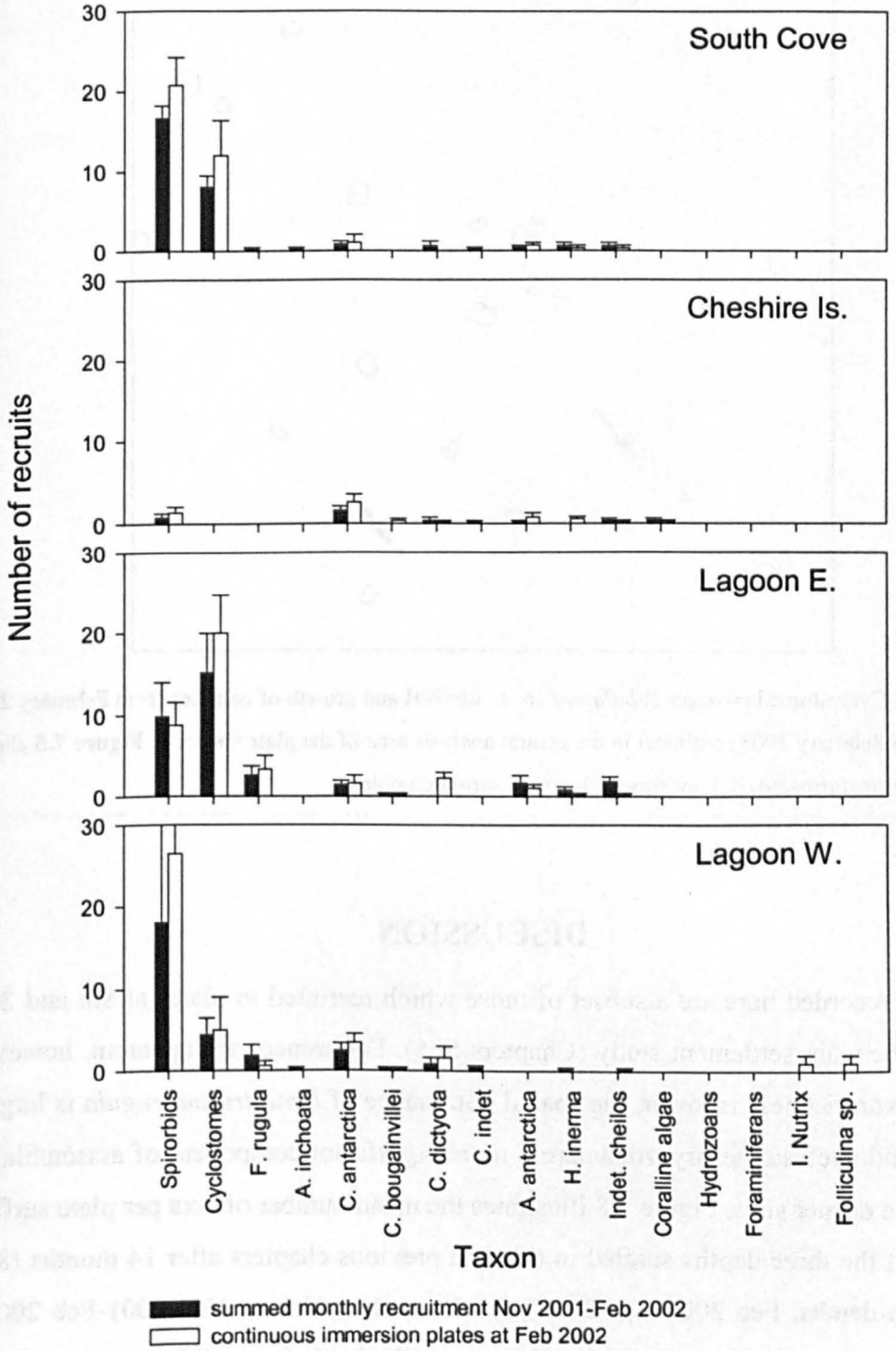


Figure 7.6 Total numbers of recruits recorded on shallow monthly-immersion plates from November 2001 – February 2002 (black bars) compared with the total number of recruits present on shallow continuous-immersion plates over the same period (open bars). n = 5, error terms 1SE. For spirorbids in Lagoon W. plot, error terms are 13.9 (monthly plate recruits) and 23.9 (continuous plate recruits)

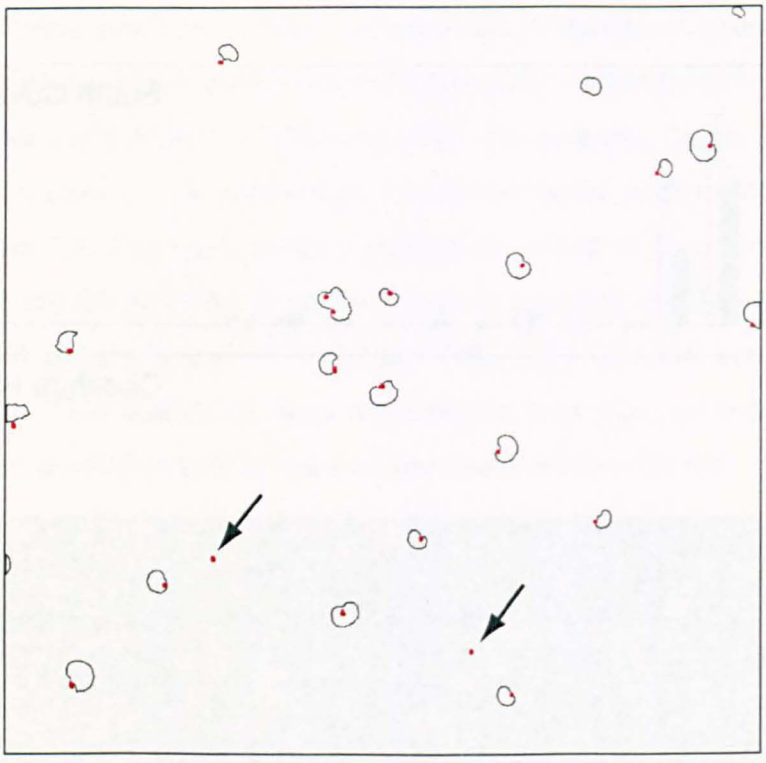


Figure 7.7 Cyclostome bryozoan *Tubulipora* sp. 1: survival and growth of colonies from February 2002 (red fill) to February 2003 (outlines) in the central analysis area of the plate shown in **Figure 7.5** above. Only 2 recruits (arrowed) did not survive between sampling points.

DISCUSSION

The taxa recorded here are a subset of those which recruited to plates at 8m and 20m sites in the main settlement study (Chapters 5, 6). Differences are apparent, however, in that taxon richness is lower, the spatial dominance of *Fenestrulina rugula* is largely absent, and cyclostome bryozoans are a more significant component of asssemblages than at the deeper sites. Figure 7.8 illustrates the mean number of taxa per plate surface at each of the three depths studied in this and previous chapters after 14 months (8 m and 20 m depths, Feb 2001-Apr 2002) or 15 months (<0.5 m, Nov 2001-Feb 2003). There is a clear increase in taxon richness with depth but valid comparisons are problematic because of the differences in total area sampled. The plate size differs between studies (100 cm^2 vs 150 cm^2) and the number of intact plates varied with depth resulting in sampled areas of 1600 cm^2, 2250 cm^2, and 2700 cm^2, in order of increasing depth. The increase in the number of taxa could, therefore, be partly a consequence of the species-area relationship (Arrhenius 1921). However,

standardisation of areas by random selection (random number generation in Microsoft Excel) of subsets of 10 plates from each depth in the main study (Figure 7.8) suggests that the decline in species richness of recruitment with decreasing depth is a real phenomenon.

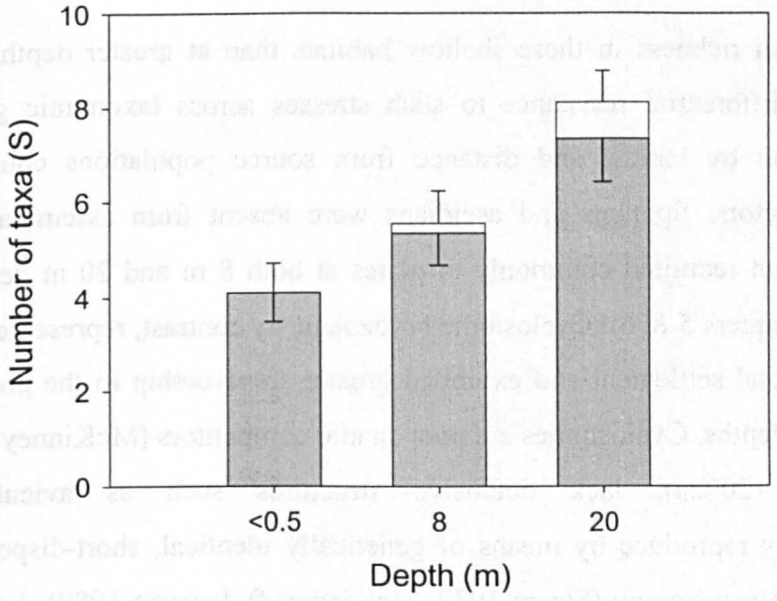


Figure 7.8 Number of sessile taxa recruiting to artificial plates immersed at three depths (<0.5m, 8m, and 20m) for 15 (<0.5 m depth) or 14 (8 m and 20 m depths) months. For 8 m and 20 m depths, filled bars show mean numbers of taxa standardised to 1500 cm^2 total area by random selection of 10 plates from each depth. Open bars show means of all plates: <0.5 m, n = 16; 8 m, n = 15; 20 m, n = 18. Total substratum areas (all plates) are1600 cm^2, 2250 cm^2, and 2700 cm^2 respectively.

Perhaps the most interesting aspects of these results are that the larvae of some sessile organisms evidently do recruit to substrata at these depths and that they survive throughout the winter. Even in microhabitats protected from physical scouring by ice, the shallow sublittoral in Antarctica has been assumed to be a harsh environment for both the larvae and the adults of marine invertebrates. In summer, the large temperature ranges associated with shallow, tidal habitats and salinity fluctuations resulting from melt water have been predicted to cause mortality of larvae (Thorson 1950). In winter, sea-ice and the formation of an 'ice-foot' extending from the littoral to below chart datum has been thought to render survival of adults unlikely due to freezing and hypersaline conditions (Barnes 1995b, 1999). The immersion period of

the plates in this study included two summers separated by a winter of unusually heavy sea-ice cover: fast-ice formed in May 2002 and cover was continuous until January 2003 with ice thicknesses >1 m over open water and ~2 m close to shore (pers obs). The present data, therefore, show that neither mortality of larvae due to salinity or temperature stress, nor of adults due to freezing during winter are barriers to colonisation of hard substrata in the immediate sublittoral.

The lower taxon richness in these shallow habitats than at greater depths might be explained by differential resistance to such stresses across taxonomic groups, but habitat selection by larvae, and distance from source populations could also be contributory factors. Sponges and ascidians were absent from assemblages in the present study but recruited commonly to plates at both 8 m and 20 m depths in the main study (Chapters 5 & 6). Cyclostome bryozoans, by contrast, represented a greater proportion of total settlement and exhibited greater survivorship in the present study than at greater depths. Cyclostomes are poor spatial competitors (McKinney & Jackson 1989, Barnes 2002a), lack defensive structures such as avicularia, and characteristically reproduce by means of genetically identical, short-dispersal larvae produced via polyembryony (Strom 1977, McKinney & Jackson 1989). Low rates of post-settlement mortality in all taxonomic groups are also indicated by the similarity between number of recruits on plates immersed continuously from November to February and the total number of settlers recorded on plates immersed at monthly intervals through the same period (Figure 7.6). Considering the higher incidence of biological disturbance affecting assemblages at 20 m than at 8 m (Chapter 6), the high survivorship observed here might be a consequence of a gradient of decreasing biological disturbance with decreasing depth. Such a gradient would make intuitive sense as assemblages of vagile taxa become more diverse and generally more abundant with depth (Chapter 3). Thus, reduced predation and competition at shallow depths might allow less-competitive 'r-selected' species to survive and proliferate.

Chapter 8 – Effects of vagile fauna on sessile assemblages

Chapter 8 – Effects of vagile fauna on sessile assemblages

INTRODUCTION

In the preceding chapters circumstantial evidence has been presented suggesting that post-settlement mortality caused by vagile macrofauna may be an important factor structuring sessile assemblages in the study area. Firstly, in the survey of surrounding biota (Chapter 3), the average population densities of the urchin *Sterechinus neumayeri* and the limpet *Nacella concinna* were found to be high (~100 inds.m^{-2}) at all study sites. The effects of grazing by urchins in other parts of the world suggested that *S. neumayeri* in particular might be expected to have significant effects on sessile benthos. Secondly, in the study of monthly recruitment to artificial plates (Chapter 5) seasonal declines in the relative abundance of recruits recorded on plate upper surfaces coincided with the early-summer resumption of feeding by *S. neumayeri* documented by Brockington et al (2001) at the same locations. Thirdly, despite appreciable levels of short-term recruitment to plate upper-surfaces in the monthly recruitment study, upper-surfaces of all the continuously immersed plates (Chapter 6) remained largely uncolonised after three years. Protected lower surfaces of these plates, by contrast, often supported diverse assemblages which, at some sites, covered up to 100 % of available area. Finally, in the study of continuously immersed settlement plates, comparisons of realised growth with potential growth patterns derived from undisturbed colonies and individuals showed that, even after three years and without pre-settlement recruitment limitation, realised growth was often minimal, suggesting considerable post-settlement mortality.

The aim here was to test experimentally the hypothesis that the feeding activities of common vagile macrofauna are a significant cause of mortality in recently established sessile assemblages. *In situ* caging and exclusion approaches involve considerable investment in dive time, are problematic in terms of cage effectiveness, and can yield equivocal results unless all effects of caging and non-target taxa can be controlled for. Instead, the choice was made to run an experiment in which assemblages were allowed to recruit and develop on artificial plates on the seabed before being exposed to grazing by one of three macrofaunal species under controlled conditions in the aquarium. The two most abundant grazing species across all study sites, *S. neumayeri*,

and *N. concinna* were chosen as test species, together with the asteroid *Odontaster validus* which is a common generalist feeder in Antarctic nearshore environments (Dayton et al. 1974, McClintock et al. 1988). All three species were frequently found on the surfaces of both monthly-immersion and continuous-immersion settlement plates in the recruitment and assemblage development studies described above.

METHODS

A total of 36 opaque black acrylic settlement plates (25 × 15 × 0.5 cm) were immersed and left *in situ* for approximately one year (deployed 3rd-5th March 2003, recovered 10th-16th February 2004) to allow colonisation by sessile encrusting fauna. On retrieval, plates were maintained in seawater at ambient temperature in the aquarium and 21 plates with the greatest colonisation were selected. Assemblages on undersurfaces of these plates were digitally photographed in a shallow seawater bath (Nikon D100 with micronikkor 60 mm lens) and the area occupied by each taxon within the central 150 cm^2 area of each plate was measured by means of image analysis software (FoveaPro 3.0 Reindeer Graphics Inc.).

Two shallow tanks with continuous through-flow of seawater at ~ 0 °C in the Bonner laboratory aquarium were used for the experiment. Cages made from 1 cm aperture plastic mesh, each large enough to accommodate one settlement plate, were suspended such that their upper edges were above water level to prevent entry or exit of vagile macrofauna. The 21 settlement plates were then randomly assigned to cages. Plates were laid flat with undersurfaces uppermost (i.e. with the more heavily colonised surface facing upwards). Adult specimens of *Sterechinus neumayeri, Nacella concinna,* and *Odontaster validus* were collected from South Cove. Each settlement plate was assigned to one of these species, resulting in 7 replicate plates per species distributed haphazardly throughout the tanks. The number of individuals introduced per plate was based on the density of these species found on natural substrata in the study area (Chapter 3). Thus, 3 *S. neumayeri* (~100 inds. m^{-2}), 3 *N. concinna* (~100 inds. m^{-2}), or 1 *O. validus* (~30 inds.m^{-2}) were introduced to each plate.

Because of the limited number of colonised plates available and the variability of colonisation on them, it was considered more useful to maintain the maximum level of replication than to run a simultaneous control treatment. However, during previous

years, similarly colonised plates held in the aquarium in the absence of macrofauna showed no reduction of sessile encrusting fauna over periods of up to 3 weeks (initial photographs followed by examination under low-power microscopy, DB personal observation). This observation provides a form of experimental control justifying the null hypothesis of no mortality in the absence of vagile macrofauna in the present experiment. Thus, it was assumed here that any significant reduction in colonised area from initial levels would be caused by grazing or predation by vagile macrofauna. Also, as the two tanks used in the experiment were immediately next to each other, identical in shape, and supplied by the same seawater feed, it was not considered appropriate to include 'tank' as a blocking factor in analyses.

Plates were exposed to vagile macrofauna for 27 d (19/02/04 to 17/03/04). They were then re-photographed and the areas covered by each taxon on each plate were measured as described above (Chapters 3, 6). Analyses were conducted on four categories of sessile encrusting fauna: all taxa combined; cheilostome bryozoans; cyclostome bryozoans, and spirorbid polychaetes. For analysis, change in colonised area was expressed as the ratio of the area occupied after exposure to macrofauna to the area occupied before exposure. Thus, a value of 1 indicates no change in area, values <1 indicate reduction in area, and values >1 indicate increase in area. Significant departures from a ratio of 1 (H_0 = no change in area) were tested for by two-tailed *t*-tests on each faunal component in each treatment. The effects of the three macrofaunal species on each of the four categories of sessile taxa were made using one-way ANOVA with macrofaunal species as the main factor and individual plates as replicates. Where the effect of macrofaunal species was significant, Tukey *post hoc* tests were used to identify differences between groups.

RESULTS

Sessile assemblages on plates recovered from the seabed consisted predominantly of spirorbid polychaetes and small colonies (~10 mm diameter) of cheilostome bryozoans, with cyclostome bryozoans and serpulid polychaetes in lower abundance. Most cheilostome colonies were *Fenestrulina rugula* but *Arachnopusia inchoata*, *Chaperiopsis protecta*, *Aimulosia antarctica*, *Celleporella antarctica*, and *Smittina* sp. were also present in low numbers. Cheilostome bryozoans and spirorbids occurred on all 21 selected plates but cyclostome bryozoans were present on only 12 plates.

After 27 days there was a significant reduction in colonised area of all components of sessile fauna on plates exposed to *S. neumayeri*, whereas colonised areas on plates exposed to the other two macrofaunal species were not significantly different from initial values (Table 8.1). On plates exposed to *S. neumayeri*, all cyclostome bryozoans, 90-100 % of cheilostome bryozoans, and 40-60 % of spirorbids had been removed, resulting in a reduction of approximately 80% in total colonised area across all taxa (Figure 8.1). Cheilostome bryozoan colonies on these plates were generally removed without trace but scars and shell remnants were visible where cyclostome bryozoans and calcareous polychaetes had been removed. All three serpulid polychaetes (each approximately 12 mm in length) present on *S. neumayeri* treatment plates were removed by urchin grazing. All sizes of spirorbid polychaetes were removed, apparently at random, and all cheilostome bryozoan species appeared to be equally vulnerable to predation.

Table 8.1 One-way ANOVA for differences between the effects of *Sterechinus neumayeri* (Sn), *Nacella concinna* (Nc), and *Odontaster validus* (Ov) on the area covered by sessile encrusting assemblages.

Taxonomic group	F	P	Tukey
All sessile taxa	28.50	<0.0001	Sn < Nc = Ov
Cheilostome bryozoans	34.89	<0.0001	Sn < Nc = Ov
Cyclostome bryozoans	6.56	0.0175	Sn < Nc = Ov
Spirorbid polychaetes	14.29	0.0002	Sn < Nc = Ov

Numerator df = 2. Residual df = 18, except cyclostome bryozoans residual df = 9.

Although statistical analysis did not indicate significant changes in area for any taxonomic grouping in *N. concinna* and *O. validus* treatments, examination of photographs taken before and after exposure to these species showed damage to both cheilostome and cyclostome colonies in the *N. concinna* treatment, and removal of some cyclostome colonies in the *O.validus* treatment. On individual plates exposed to *N. concinna*, total areas of cheilostome and cyclostome bryozoans were reduced by up to 20 % but the colonies affected suffered partial damage, rather than being completely removed, and the majority of colonies were apparently unaffected. There was no evidence of mortality among spirorbid polychaetes. On plates exposed to *O. validus*, only cyclostome bryozoans were noticeably reduced, but this effect was not consistent

across replicate plates. Cheilostome bryozoan colonies were unchanged in area on these plates but individual spirorbid polychaetes and the two serpulid polychaetes present on these plates had grown during the experiment.

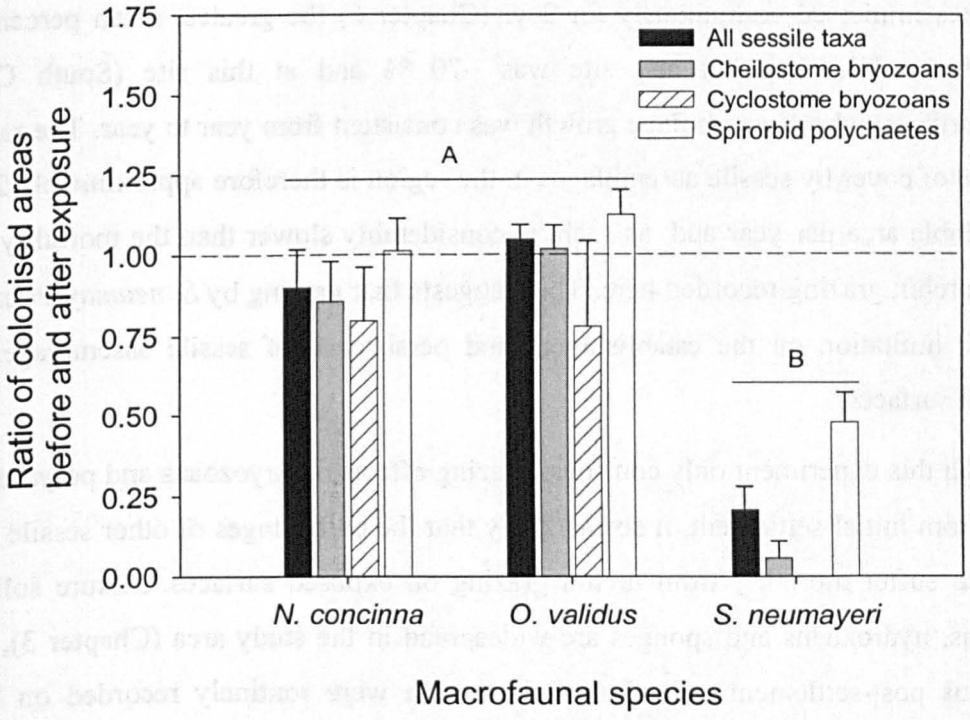


Figure 8.1 Effect of *Nacella concinna, Sterechinus neumayeri,* and *Odontaster validus* on sessile epifauna. Assemblages established on acrylic plates over ~1yr were exposed to one of the three vagile macrofaunal species for 27 d. Data are ratios of area covered before exposure to area covered after exposure. Thus, values <1 indicate mortality, values of 1 indicate no change in area, and values >1 indicate growth. Bars show means, n = 7, except cyclostome bryozoans n = 4, error terms are 1SE. The lines A and B group results which are not significantly different in analyses of each taxonomic group separately (one-way ANOVA and Tukey *post hoc* tests). Means in group B are the only ones which are significantly < 1 (*t*-tests $P < 0.05$).

DISCUSSION

These results show that grazing by *Sterechinus neumayeri* caused substantial mortality of fauna in sessile assemblages established over 1 year, and that any effects of *Nacella concinna*, and *Odontaster validus* were minor by comparison. The mortality caused by *S. neumayeri* grazing was not taxon-specific and after 1 year of growth neither

bryozoans nor calcareous polychaetes had achieved a refuge in size from such predation.

On substrata exposed to *Sterechinus* grazing for one month, the mean reduction in total area covered by sessile fauna was approximately 80 %. Thus it might be expected that fauna on these plates would have been removed completely in less than two months. On plates immersed continuously for 3 yr (Chapter 6) the greatest mean percentage cover by sessile fauna at any site was ~70 % and at this site (South Cove, undersurfaces) whole-assemblage growth was consistent from year to year. The rate of increase of cover by sessile assemblages in the region is therefore approximately 25 % of available area per year and, as such, is considerably slower than the mortality rate due to urchin grazing recorded here. This suggests that grazing by *S. neumayeri* exerts a major limitation on the establishment and persistence of sessile assemblages on exposed surfaces.

Although this experiment only considers grazing effects on bryozoans and polychaetes at 1yr from initial settlement, it seems likely that the early stages of other sessile taxa will also suffer mortality from urchin grazing on exposed surfaces. Mature solitary ascidians, hydrozoans and sponges are widespread in the study area (Chapter 3), and numerous post-settlement juveniles of these taxa were routinely recorded on both upper and lower surfaces of monthly-immersion settlement plates (Chapter 5) during 2002-3. However, none of these taxa were present on the upper surfaces of continuous-immersion plates after 3 yr and only occasional hydrozoan and sponge recruits survived on undersurfaces after this time. From the results of the present experiment, it seems likely that the significant post-settlement mortality on exposed upper surfaces indicated by these observations may be caused in large part by the grazing activities of *S. neumayeri*. Some mortality of bryozoan colonies due to grazing by *N. concinna* was also observed, however, and although the effects were not statistically significant by comparison with *S. neumayeri* grazing, the ability of *Nacella* to remove mature bryozoan autozooids suggests that this species too may be a cause of mortality in the period immediately following settlement.

In previous studies, *Sterechinus neumayeri* has been characterised as a consumer of phytodetritus, diatoms, and algae (McClintock 1994, Brey et al. 1995, Brockington et al. 2001). However, year-round gut content analyses of populations at Anvers Island

(Brand 1976, 1980) showed that up to a third of their diet consisted of bryozoans, spirorbids and hydrozoans, with bryozoans becoming more important during winter. The present results confirm that *S. neumayeri* consumes a range of sessile fauna and, as the availability of macroalgal food is more limited at the latitude of the present study (Moe & DeLaca 1976, Wiencke 1996), it might be expected that sessile fauna would constitute an even larger proportion of the diet than at Anvers Island. This may have a bearing on the conclusion of Brockington et al (2001) that *S. neumayeri* does not feed during winter. Winter cessation of feeding was demonstrated by seasonal decreases in faecal egestion rates, gut mass, and activity in adult specimens of approximately 30mm in test diameter and, for individuals of this size, is supported by my own observations. However, during the continuous-immersion colonisation study above (Chapter 6), small specimens <10 mm in test diameter (and thus able to enter the space between the lower surfaces of plates and the base panel) remained active throughout the winter and grazed faunal assemblages on plate undersurfaces. This suggests that winter cessation of feeding in larger individuals may be related to a lack of food sources once the summer input of phytoplankton and benthic diatoms on exposed upper surfaces has been consumed. Smaller individuals, by contrast, are able to exploit sessile faunal assemblages in cryptic habitats between and under rocks and thus to continue foraging through the winter.

As *Sterechinus neumayeri* appears to be undiscriminating in its grazing (Brand 1980, this study), it is also likely to consume early recruits of vagile taxa. Grazing by this species in the study area may also, therefore, limit populations of a wide range of vagile, as well as sessile, taxa. Dayton et al. (1974) have suggested that such effects are caused by predation on settling larvae by high densities of *Odontaster validus* in McMurdo Sound. An extension of this is that *S. neumayeri* presumably also consumes early conspecific recruits and thus that there may be an element of self-regulation in urchin populations. This is particularly likely to occur in areas where adult population-densities are high and physical refugia are scarce, such as in the heavily ice-scoured shallow sublittoral above ~10m depth. At greater depths (> ~15 m) sessile assemblages are more developed and benthic habitats are, therefore, structurally more heterogeneous, affording greater potential for settling larvae to escape grazing. Brockington (2001a) found that urchins <10 mm in test diameter were absent from the shallow sublittoral in South Cove, where larger adults (>20 mm diameter) were

abundant. At greater depths, however, small individuals were abundant. This pattern could be explained by the argument above if settlement does not vary with depth. Alternatively, this size distribution could be caused by greater larval settlement at depth followed by upward migration with growth. It is intriguing, however, that Brey *et al.* (1995) and others have noted the absence of small individuals of *S. neumayeri* at McMurdo Sound. This might be evidence for the hypothesis of population limitation through predation on settling larvae (Dayton et al. 1974) but the absence of late-stage echinoplutei in plankton tows observed by Bosch et al. (1987) suggests that mortality or offshore transport in the pelagic phase may also be significant.

While grazing by urchins and limpets is likely to be the major factor influencing mortality on exposed hard substrata in the study area, other grazing taxa, such as the gastropod *Margarella antarctica* and the limpet *Iothia coppingeri* were also locally abundant. Due to their smaller size these species may exert a proportionately greater influence on recruitment in cryptic habitats. Perhaps more significant in terms of the prevention of competitive exclusion in mature assemblages, however, is the presence of selective predators. Opisthobranch molluscs, pycnogonids, isopods and nemerteans were present at all study sites and some species, at least, are known to be specialist predators of sessile taxa (Barnes & Bullough 1996). In the continuous immersion colonisation study here (Chapter 6) several instances were observed in which established colonies of *Arachnopusia inchoata* were completely removed, possibly by the opisthobranch *Pseudotritonia gracilidens* (Barnes & Bullough 1996). However, the margins of *Fenestrulina rugula* colonies which were overgrown by *A. inchoata* remained undamaged in these events, indicating highly selective predation (Figure 8.2). As *A. inchoata* is one of the principal competitive dominants in these assemblages, such predation is evidently a mechanism by which spatial domination and competitive exclusion can be prevented and coexistence prolonged.

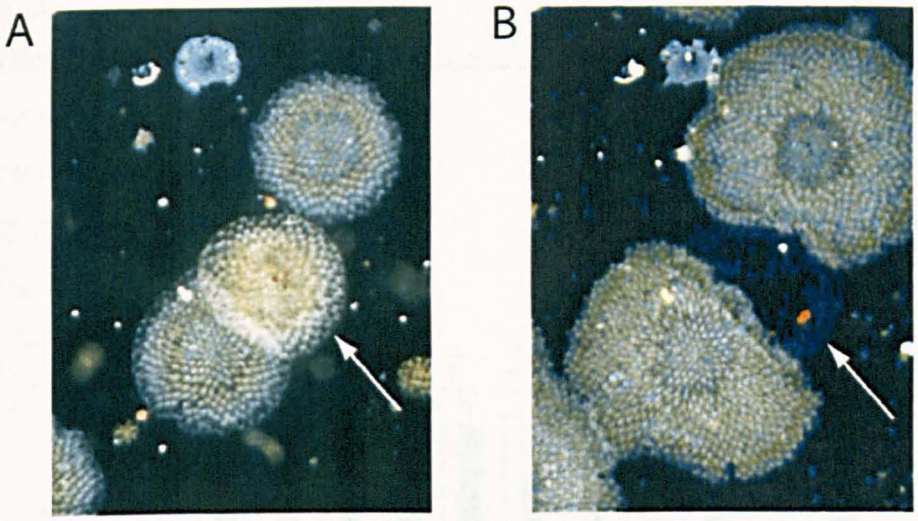


Figure 8.2 Selective predation on *Arachnopusia inchoata*. A: March 2003, *A. inchoata* colony (arrowed) overgrowing *Fenestrulina rugula*. B: the same area in February 2004, showing the scar (arrowed) where the *A. inchoata* colony has been removed (detail from the undersurface of plate 6, South Cove 20 m site).

In light of the levels of mortality caused by vagile species, seasonal variations in their activities might also be expected to be important in the dynamics of sessile assemblages. Figure 8.3 shows the numbers of vagile taxa (echinoderms, molluscs, polychaetes, and pycnogonids) visible in photographs of the upper surfaces of continuously immersed settlement plates taken at monthly intervals through the year April 2002 to March 2003 (Chapter 6). The increase in activity between November and March evident here suggests that mortality of sessile organisms from grazing and predation is likely to be greater in summer than during winter. In Chapter 5 it was proposed that the trend for winter settlement in sessile taxa could be evidence of an adaptive response to increased mortality of larvae and recruits in summer caused by seasonal (summer) feeding of suspension and deposit feeding taxa. The inverse correlation between the seasonal activity of vagile taxa here (Figure 8.3) and winter settlement of sessile taxa seen at 20 m in the short-term recruitment study (Chapter 5) provides some circumstantial support for this. However, the present data are insufficient to resolve this question and more specific studies would be needed to test the hypothesis.

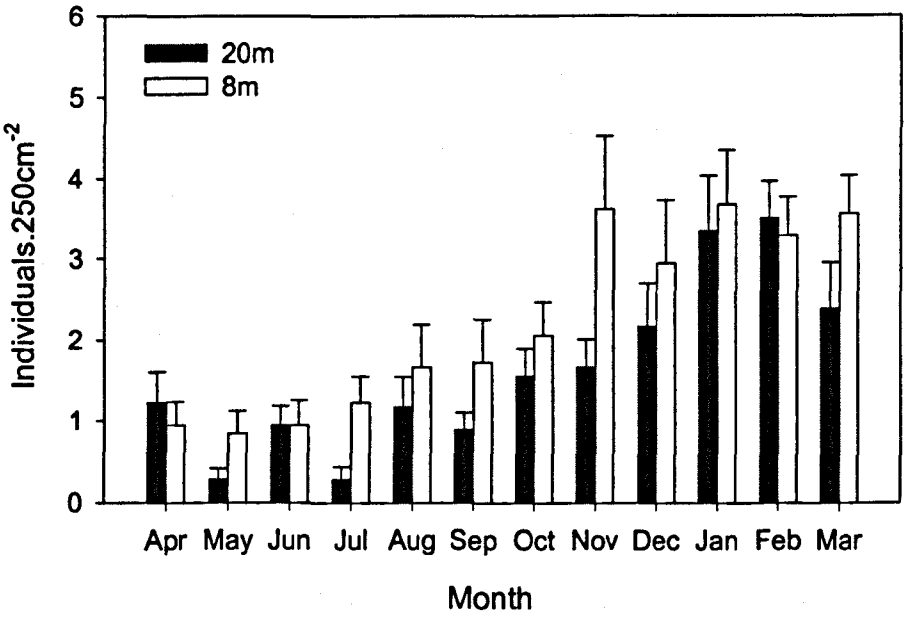


Figure 8.3 Vagile macrofauna (all species) recorded on the upper surfaces of continuous-immersion settlement plates at two depths (8 m, 20 m) during the year 2002-3. Counts include all individuals visible in photographs of the entire plate surface (250 cm^2). Bars show means across all locations at each depth, n = 18, error terms 1SE.

Chapter 9 – Seasonality of planktonic larvae

Chapter 9 – Seasonality of planktonic larvae

INTRODUCTION

The preceding chapters have described established benthic assemblages in the study area, the seasonal and spatial patterns of recruitment by sessile taxa, and the interactions between growth rates and mortality that dominate subsequent development. Linking each of these, however, and central to any understanding of how assemblages are established and maintained over all spatial and temporal scales, is the larval phase of the life cycle.

Although marine invertebrate larvae have been studied for centuries, there have been very few year-round studies of seasonal abundance, and fewer still which deal with whole assemblages rather than single species or taxonomic groups. The work of Thorson (1936, 1946) in Greenland and Denmark, and the survey conducted at Signy Island in the South Orkney Islands by Stanwell-Smith et al. (1999) are the only published studies I am aware of which detail the larvae of all meroplanktonic taxa found throughout an annual cycle. An unpublished study of zooplankton at Ellis Fjord in East Antarctica, however, recorded the seasonal abundances of four major meroplanktonic types over one year (Kirkwood 1994). The paucity of such studies is probably a consequence of two main factors. Firstly, meroplanktonic larvae are generally present in low densities by comparison with holoplanktonic taxa, such as copepods, and may be patchily distributed in both space and time. Such distributions cause considerable difficulties for the design of representative sampling strategies (Avois et al. 2000) and the processing of samples. Secondly, by definition, the larva is an early developmental stage which precedes metamorphosis into the adult form, and thus has little or no physical resemblance to the adult. Furthermore, many larval types develop through two or more stages before final metamorphosis (e.g. annelid trochophores become nectochaete larvae, molluscan trochophores become veliger larvae, and asteroid bipinnaria become brachiolaria larvae), leading to potential over-estimation of taxonomic diversity when identifications are based on the principle of morphologically defined operational taxonomic units (OTUs, *sensu* Stanwell-Smith et al. 1999). Adding further complication, some larval types are common to more than one phylum (e.g. trochophore larvae are present in Mollusca, Annelida, and Sipuncula)

and therefore even aggregation to higher taxonomic levels does not ensure accuracy of identification. Thus, problems with the reliable identification of larvae, and therefore with relating larval distributions to adult populations, represent the greatest obstacle to progress in this field (Mullineaux et al. 1995). Molecular techniques have great potential for resolving these difficulties but, to date, their application has been limited (Olson et al. 1991, Hare et al. 2000, Deagle et al. 2003)

Difficulties of identification also have a bearing on the continuing debate over the relative prevalence of planktonic and non-planktonic developmental modes with latitude. The paradigm that planktonic, particularly planktotrophic, larvae are selected against in high latitudes (Thorson's Rule: Mileikovsky 1971) has been largely undermined by recent studies in the Antarctic and South America (Pearse et al. 1991b, Hain & Arnaud 1992, Stanwell-Smith et al. 1999, Gallardo & Penchaszadch 2001, and reviewed by Pearse & Lockhart 2004). However, with the exception of Stanwell-Smith et al. (1999), these studies are of specific taxonomic groups rather than entire larval assemblages. In studies such as these, larvae may be spawned in aquaria, larval mode may be inferred from characteristics of the adult or egg, or where larvae have been sampled in the water column, confirmation of identification is possible through comparison with larvae spawned from adults of the target species in the laboratory. Without recourse to these methods of identification, general surveys of whole larval assemblages are restricted to grouping by larval type (e.g. trochophore, nectochaete, pilidium), by OTUs, or by aggregating to higher taxonomic groups based on the known distribution of larval types between phyla or classes. Such classifications, therefore, inevitably involve subjective decisions and considerable scope for error. A consequence of this uncertainty is that comparisons between surveys of larval assemblages can only be at the most general level and rigorous comparisons between regions regarding the numbers of species with planktonic larvae are problematic.

These problems notwithstanding, the scarcity of data on the seasonality, abundance and distribution of meroplanktonic larvae at any latitude is such that even general comparisons are of value. The objective of the present study was to conduct a survey directly comparable with that of Stanwell-Smith et al. (1999) but at a latitude more representative of coastal waters around the Antarctic continent. By sampling at monthly intervals through more than one full year, the survey aimed to assess the

diversity, seasonality, and spatial variability of occurrence of the planktonic larvae of benthic invertebrates in the study area.

METHODS

Net design

Plankton were sampled by means of a diver-towed net as described by Stanwell-Smith et al. (1999). The apparatus consisted of a square aluminium frame (0.5 m x 0.5 m) supporting the mouth of a 2 m long conical net made of 100 μm plankton mesh with a 90 mm diameter cod-end. Handles on either side of the frame allowed two divers to tow the net close to the substratum. Two flowmeters (General Oceanics 2030 R6 with low-velocity rotors) were mounted on the frame; one in the centre of the net mouth and one externally. Distance travelled through the water was calculated from the outer flowmeter readings, the volume of water passing through the net was calculated from the inner flowmeter readings, and comparison between the two enabled calculation of filtration efficiency. Cod-end containers were 1litre plastic screw-fit bottles which could be removed and sealed underwater. To minimise reduction in filtration efficiency caused by stagnation within the cod-end container, the containers were modified from those used by Stanwell-Smith et al. (1999) by the addition of twelve, 20 mm diameter, 100 μm mesh-covered holes in the upper half of the container body.

Net ratios (length:mouth width) of >6 are optimal for reduced clogging and hence increased filtration efficiency (Tranter & Heron 1967). However, the ratio of the net used here is 4 and, therefore, is not optimal for high filtration efficiency. Increases in efficiency can also be gained by the insertion of a parallel-sided section between the mouth and the main conical section of the net (Tranter & Heron 1967). These improvements to the net were not made in the present study for two reasons. Firstly, it was impractical (in terms of time and expense) to have new nets made and tested before the start of the fieldwork. Secondly, by using the same apparatus as was used by Stanwell-Smith et al. (1999), data from the two studies would be directly comparable. For future work, however, the adoption of these modifications would be advisable.

Sampling

Monthly plankton samples were taken at each of the study sites (Section 1). Thus, samples were taken from each of two depths (6 m, 20 m) at each of the three locations

(Hangar Cove, South Cove, Anchorage). Because of dive-profile constraints, however, the shallow tows were made at 6m, rather than at 8 m where the arrays of settlement plates were installed (Chapter 5). All tows were made close (<2 m) to the substratum along the nominal isobath, using the settlement plate array at each site as the central reference point for the tow.

Following removal and sealing of the cod-end container at the end of each tow, the net was flushed by introducing compressed air from a SCUBA regulator into the net mouth: expansion of the rising air rapidly flushed the remaining contents out through the open cod-end. During the ascent from 20 m to 6 m the net was towed with no cod-end container attached to ensure further flushing and to prevent cross-contamination between samples from different depths. In initial tests during summer the net became clogged (the inner flowmeter stopped rotating) by dense phytoplankton blooms after ~25 m tow distance. Spare cod-end containers were, therefore, carried and when clogging occurred the tow was stopped, the full container was removed and replaced with a second container, and the tow resumed.

For the first 6 months of the study, one tow was made at each site in each month (i.e. 1 tow at 20 m and 1 tow at 6 m at each location) resulting in a total of 6 samples per month. The lack of replication inherent in this design, however, limited the potential for comparisons between depths. When diving recommenced in 2002, therefore, 2 separate tows were made at each depth at each location. The two tows were made in opposite directions along the same track during a single dive and thus are arguably not fully independent replicates. However, this was the most pragmatic solution to maximising sampling effort within the constraints of available dive time. In the first 6 months of sampling (2001) tows were of 2 minutes duration when phytoplankton blooms were dense (March and April) but were increased to 3 minutes in the winter months (May–September). This was done a) because the physical effort required to tow the net was greater during phytoplankton blooms, and b) to increase sample volume during winter when it was assumed that larval densities would be lower. On the resumption of the survey in March 2002, however, all tows were timed to be of 2 minutes duration. Anchorage sites were inaccessible because of ice conditions in July and August 2001, and in May and November 2002. In these months, extra tows were made at either Hangar Cove or South Cove.

Tow speed

Stanwell-Smith et al. (1999) deduced from Tranter & Heron (1967) that there is a monotonic increase in filtration efficiency with increasing tow speed at speeds of up to 1 knot (~0.5 ms^{-1}). However, Tranter & Heron (1967) worked with ship-towed nets and tow speeds of <0.5 ms^{-1} were below the reliable response threshold of the flowmeters they used. The maximum sustainable swimming speed of SCUBA divers varies with individuals and conditions but is somewhat less than 1 ms^{-1}. In cold water and with the added drag of the towed net the maintenance of high tow speeds increases the probability of dives being aborted due to headache, breathlessness and nausea associated with CO_2 accumulation, and free-flows caused by freezing of SCUBA regulators. For these reasons, maintaining high tow speeds was considered to be less important than the reliable and safe completion of sampling. However, all tows were conducted by the same three divers throughout the study (D. A. B. was present on all tows) and, therefore, speeds were relatively consistent throughout. Linear regression analyses of filtration efficiency against tow speed were used at intervals during the study to assess the influence of towing speed on net filtration efficiency.

Limitations of the survey design

The survey of planktonic larvae followed the basic experimental design used in the settlement plate studies (Chapter 4). However, as noted above, practical limitations dictated that the number of replicate tows at each site was minimal (2 plankton samples as opposed to 6 replicate settlement plates at each site). The low number of samples at each site, and the lack of replication of depth sites within each location, allowed only limited scope for detailed spatial analysis. The decision to sample at 3 locations, rather than to increase replication by reducing the overall number of survey locations, was made for two reasons. Firstly, as an initial base-line survey of the area it was considered more useful to record general patterns across a wider geographic area than detailed distributions at a single location which may not be characteristic of the local area. Secondly, by sampling planktonic larvae at each of the study sites in parallel with the deployment of settlement plates at these sites, direct comparisons could be made between the availability of larvae in the water column and the timing of recruitment.

Sample analysis

Immediately after each dive, samples were returned to the aquarium and decanted into individual 1 litre glass beakers. These were suspended in a tank supplied with flowing seawater at ambient temperature. Samples were aerated constantly to ensure adequate oxygenation and to maintain plankton in suspension, and all samples were examined within 24 h of collection. Examination was by low-power (10-63 ×) and high-power (100-400 ×) light microscopy and all larvae were alive at the time of examination. Larvae of marine invertebrates rarely possess skeletal structures (Young 2002) and are often best discerned by their characteristic motion (D. A. B. personal observation). Preservation of samples, therefore, can cause many smaller larvae and those without characteristic shape, such as planulae, to be missed.

All larvae in all samples were recorded. To obtain suitable quantities for microscopy, each 1 litre sample was divided into a series of concentrated subsamples by filtration through a 100 μm mesh-ended perspex cylinder suspended in a seawater-filled beaker. The number of subsamples varied depending on the density of plankton in the sample: during the summer phytoplankton bloom up to 20 subsamples were required but during the winter only 5-10. Each subsample in turn was washed, with a minimum quantity of seawater, into a 60 mm diameter, optically flat, glass petri dish. This dish was placed in a larger petri dish and surrounded by crushed ice to maintain larvae alive during examination under the microscope. Larvae were often highly mobile and accuracy of counts was ensured by pipetting individuals out of the subsample as they were counted, and into a separate dish for each taxon. This technique also enabled confirmation of identifications within taxa as all individuals of each putative taxon could be examined alongside each other once the whole sample had been sorted. All new larval morphotypes were photographed digitally and a library of images of each taxon was maintained throughout the study to enable retrospective comparison of identifications. Highly mobile taxa were anaesthetised by the addition of small quantities (up to ~20 % of the total seawater volume) of 7.5 % MgCl solution.

Taxon identification

Each new larval morphotype was assigned an identification code consisting of the date of the sample in which it was first found and a sequential letter. Thus, [1.1.02 C] would denote the third new larval type found in samples taken on the 1st of January

2002. Each new type was compared to images of all previous types and where there were clear similarities suggesting that they were successive developmental stages of the same taxon, types were aggregated. Once this process of cross-checking and aggregation was complete, all remaining larval morphotypes (OTUs) were numbered sequentially in order of first appearance. These taxon numbers were used as the primary identifiers in all subsequent analyses. Wherever identification to class or phylum could be made with reasonable certainty following descriptions in the literature, OTUs were grouped accordingly. The aggregation process was hierarchical and thus the original sample reference codes for all larvae were retained throughout, allowing identifications to be reviewed should more taxonomic information become available. As the survey was concerned specifically with the larvae of benthic taxa, all larvae of holoplanktonic taxa (e.g. pteropod mollusc veligers, ctenophore cydippid larvae, *Tomopteris* sp. nectochaetes, copepod nauplii) and all non-larval forms (e.g. ostracods, isopod juveniles) were excluded from analyses. OTUs are listed in Appendix B and representative images are filed on the attached CD.

Statistical analysis

Data were recorded as numbers of individuals per taxon in each sample and then standardised to uniform sample size of 5 m^3 (following Stanwell-Smith et al. 1999). As the number of samples at each site in each month was small (2002, n = 1; 2002-3, n = 2), and experimental sites were not replicated at each depth within each location, the power of statistical tests was too low for reliable comparisons of the effects of depth and location factors within months. Therefore, samples from all months were pooled in initial analyses to enable broad comparison of assemblages by depth and location over the entire study period. Prior to these analyses, data from the two tows at each depth through the second year of the study (2002-3) were averaged. This was done to guard against spurious precision arising from the potential pseudoreplication noted above. Two factor ANOVA was used to test for differences in the mean total number of taxa (OTUs) and the mean total number of individuals by depth and location. Total numbers of individuals required $\log_{10}x$ transformation to conform to assumptions of normality and homoscedascicity.

A multivariate two-way crossed analysis of similarities (ANOSIM, Clarke & Warwick 2001) was used to test for differences in whole assemblage composition between

depths and locations in each year of the study (i.e. 2001 and 2002-3). ANOSIM is a permutation-based significance test and was conducted on a matrix of Bray-Curtis rank similarities between samples. Similarities were calculated from square root-transformed abundance data. In this analysis, larval assemblages from 6 m and 20 m depths were compared by pooling samples across all locations, and assemblages at each location were compared by pooling samples from both depths.

Seasonal variations in whole-assemblage composition were explored graphically by multi-dimensional scaling (MDS) ordination of Bray-Curtis similarities between assemblages averaged across all samples in each month. Seasonal variations in the abundances of larvae are presented as plots of mean monthly abundance of OTUs aggregated to class level.

An index based on the coefficient of variation (CV = standard deviation/mean) was devised to quantify the relative ubiquity of each larval taxon. For each taxon, in each month in which it occurred, CV was calculated across all samples from all locations. To ensure consistency of sampling, only data from the second year of the study were used, thus, n = 12 samples per month. The index was calculated as:

$$Ub = 1 - \left(\frac{CV_a}{CV_{\max}} \right) \qquad \text{Equation 9.1}$$

where CV_a is the coefficient of variation calculated for taxon a, CV_{max} is the maximum value of CV calculated for any taxon in the data set, and Ub is the index of ubiquity. The coefficient of variation increases as distributions become less even (for taxa with the same mean abundances, more patchy distributions result in higher SD and therefore higher CV). By dividing CV values by the maximum value, the index is constrained to a range from 0 to 1, and by subtracting the resultant values from 1, higher values of Ub correspond to greater ubiquity. Thus, a larval taxon present in equal abundance in all samples at all locations (SD = 0) would have a Ub of 1, whereas a taxon which occurred in only one sample would have a Ub of 0. Ub was calculated for each taxon in each month in which it occurred. However, the majority of taxa were seasonal in occurrence and distributions were more variable at the beginning and end of these periods of occurrence, resulting in high variance of Ub values. Therefore, the maximum value of the index (Ub_{max}) for each taxon was used as the relative measure

of ubiquity. Where individual taxa are aggregated to higher groupings for analyses (Figure 9.7-9), Ub_{max} is averaged over all OTUs included in each group.

RESULTS

Tow data

A total of 184 tows were analysed over the 18 months of the study, sampling a total volume of 1,464 m^3. The mean monthly volume sampled was 81.4 ± 0.69 m^3, and the mean tow volume was 7.7 ± 0.02 m^3. Individual tows covered a mean distance of 54 ± 1 m at a mean speed of 0.42 ± 0.01 ms^{-1} and overall mean filtration efficiency was 58.7 ± 1.6%. However, filtration rates were consistently <50 % from January–April, during the phytoplankton bloom, and >50 % outside of this period. Linear regressions of net filtration efficiency against tow speed for each of these periods separately (Figure 9.1) indicated a significant trend for decrease in filtration efficiency with increasing tow speed outside of the summer phytoplankton bloom (ANOVA $F_{1, 111} = 44.3$, $P < 0.001$) and a non-significant relationship during the bloom (ANOVA $F_{1, 63} = 3.92$, $P = 0.052$). For all quantitative analyses larval abundances were standardised to 5 m^3 sample volume.

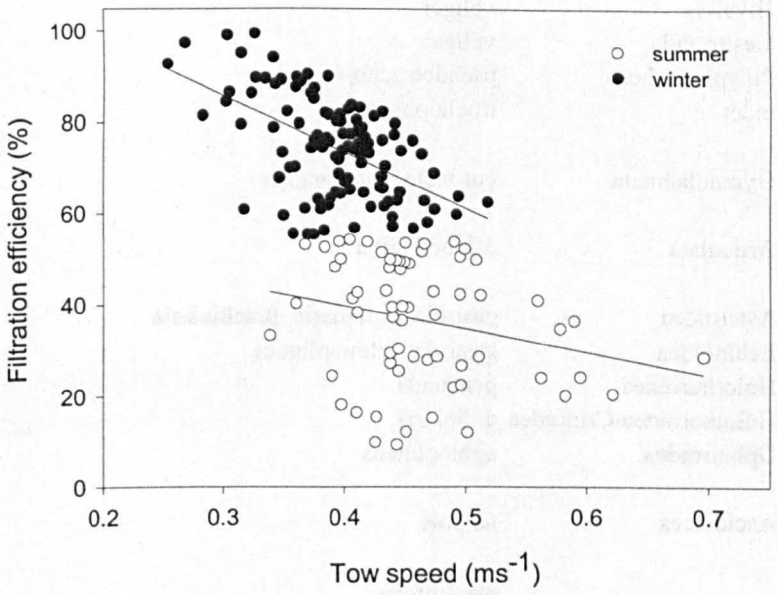


Figure 9.1 Plankton net filtration efficiency in relation to tow speed in winter (April – November; filled symbols) and during the summer phytoplankton bloom (December – March; open symbols. Regression lines: winter, $r^2 = 0.29$, $P < 0.01$; summer, $r^2 = 0.06$, $P = 0.52$.

Diversity

A total of 116 morphologically distinct larval types were recorded. However, some of these were evidently successive stages of single taxa. When these stages were aggregated to single taxa, the total number of operationally defined taxa (OTUs, *sensu* Stanwell-Smith et al. 1999) was 99, representing at least 11 phyla and 16 classes (Table 9.1).

Table 9.1 Planktonic larvae of benthic marine invertebrates. Larval types, feeding modes (L, lecithotropic; P, planktotrophic), and numbers of operationally-defined taxonomic units (OTUs) by phylum and class, together with unidentified OTUs classified by larval type.

Phylum	Class	Larval types	Mode	OTUs
Porifera	Demospongiae	parenchymella	L	4
Cnidaria	Anthozoa	planula	L	3
	Hydrozoa	Planula, actinula, medusa	L, P	5
Platyhelminthes	Turbellaria	Müller	L	1
Nemertea	Anopla	Pilidium, metamorphosing juvenile	P	3
Echiura/Sipuncula		trochophore/pelagosphera	P	3
Annelida	Polychaeta	trochophore, metatrochophore, nectochaete	P	24
Mollusca	Bivalvia	veliger	P	2
	Gastropoda	veliger	P	5
	Polyplacophora	pseudotrochophora	?	1
	indet	trochophore	?	3
Bryozoa	Gymnolaemata	coronate, cyphonautes	L, P	2
Brachiopoda	Articulata	3-lobed larva	L	1
Echinodermata	Asteroidea	gastrula, bipinnaria, brachiolaria	P	3
	Echinoidea	gastrula, echinopluteus	P	1
	Holothuroidea	pentacula	L	3
	Holothuroidea/Crinoidea	doliolaria	L	3
	Ophiuroidea	ophiopluteus	P	1
Chordata	Ascidiacea	tadpole	L	3
Unidentified taxa		planuliform	L	8
		trochophore	P	6
		gastrula	?	2
		other	?	13
Total				99

Uncertainties of classification arose with the phyla Echiura and Sipuncula, where descriptions in the literature indicated contradictory identifications, and with doliolaria larvae of echinoderms, which may represent either of the classes Holothuroidea and Crinoidea. Twenty-nine OTUs from the total of 99 could not be classified reliably, even at phylum level, and thus it is possible that some of these are not larvae of benthic taxa. It is also possible, despite the aggregations described above, that some of the classified OTUs still represent different developmental stages of single taxa or, conversely, that some represent more than one species. The total of 99 OTUs therefore is at best an estimate of total species-level larval diversity of benthic invertebrates in the area. However, every attempt was made to be conservative in assigning specimens to new OTUs. For instance, there was considerable variability in the shapes and sizes of nemertean pilidia. These may, therefore, have represented several species but only 2 OTUs could be reliably discriminated between on the basis of appearance alone. Despite this conservative approach, taxon accumulation curves for the entire data set do not reach an asymptote after 184 samples taken over 1.5 yr (Figure 9.2), indicating that the actual diversity of meroplantonic larvae may be higher than recorded here.

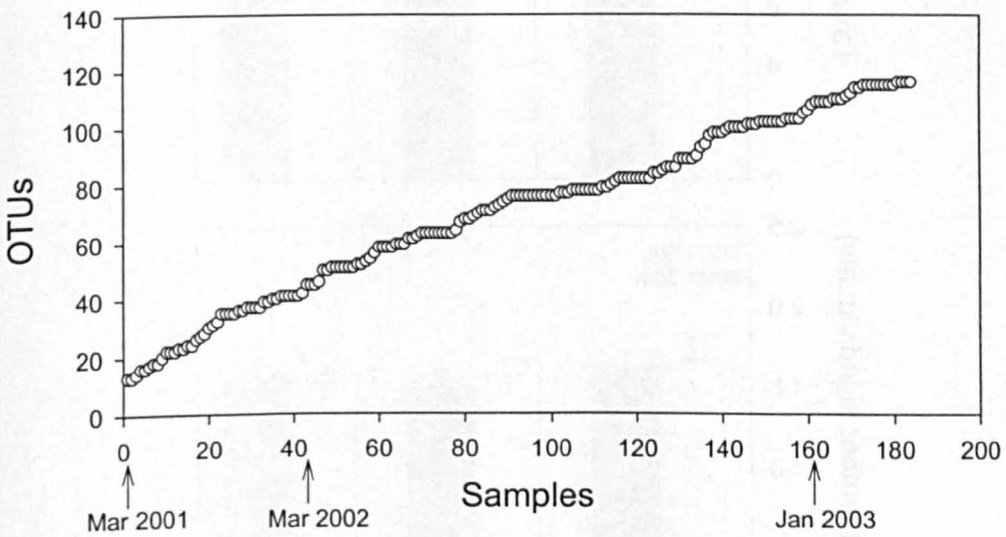


Figure 9.2 Taxon accumulation curve for larvae of benthic invertebrates caught in plankton tows from March to August 2001 (samples 1-42), and from March 2002 to February 2003 (samples 43-184). Note, the total of 116 OTUs here includes more than one developmental stage of some taxa (e.g. asteroid gastrula, bipinnaria, and brachiolaria stages). For subsequent analyses such stages are aggregated where possible to give a more conservative estimate of taxon richness (see Table 1).

Spatial distribution

No statistically significant differences between depths or locations were detected in either the total number of taxa or the total number of individuals, despite a non-significant trend for lower numbers of taxa in tows at 6 m than at 20 m (Figure 9.3) (ANOVA, $P > 0.05$, Table 9.2). ANOSIM tests of multivariate assemblage structure also showed no significant differences by depth or location (Table 9.3). However, many taxa were recorded in very low numbers; often only once through the whole study (36 % of all taxa occurred in only one sample and at densities of <5 inds.5m^{-3}), and such analyses were therefore influenced by the more abundant taxa. Furthermore, some taxa, such as bryozoan coronate larvae, were recorded at all sites but in abundances which were highly variable, even between consecutive tows in a single dive, indicating patchy spatial and temporal distributions.

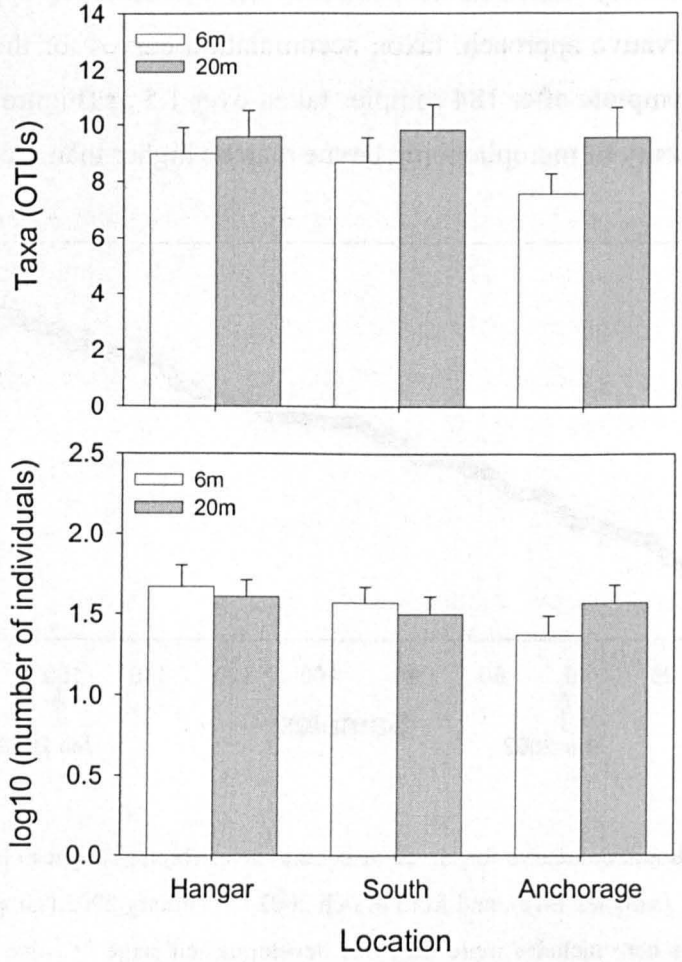


Figure 9.3 Total number of taxa (OTUs) and total number of individuals of invertebrate larvae in plankton tows from 6 m and 20 m depths at each of the study locations. All data from Feb 2001 to Feb 2003 are included. Replicate tows at each site (i.e. depth × location) taken during the second year of the

study are averaged in this analysis so that there is only one data point from each site in each month of the study. Values are means, error terms 1SE. Hangar, n = 19, South, n = 21, Anchorage, n = 16.

Table 9.2 ANOVA tables for comparisons between larval assemblages by depth (6m, 20m) and location (Hangar, South, Anchorage). A, total number of taxa (OTUs); B, total number of individuals. Data are pooled over all months of the study. Location is treated as a random factor and no test of depth/location interaction is possible.

A. Total number of larval taxa (OTUs)

	DF	Sum of Squares	Mean Square	F	P
Depth	1	41.04	41.04	2.68	0.10
Location	2	10.04	5.02	0.33	0.72
Residual	112	1713.41	15.30		

B. Log_{10}(Total number of individual larvae)

	DF	Sum of Squares	Mean Square	F	P
Depth	1	0.0001	0.0001	0.00	0.98
Location	2	0.3463	0.1732	0.73	0.48
Residual	112	26.3943	0.2357		

Table 9.3 *R*-values and significance (*P*) from two-way crossed analyses of similarity (ANOSIM) analyses comparing depths (6 m, 20 m) and locations (Hangar, South, Anchorage). Analyses include all samples in each of the two years: (9999 permutations in all comparisons. Tests are conducted on a matrix of Bray-Curtis similarities calculated from square root-transformed data).

Year	Comparison	*R*	*P*
2001	Depth	-0.100	0.99
	Hangar v South	-0.014	0.53
	Hangar v Anchorage	-0.069	0.79
	South v Anchorage	-0.050	0.68
2002-3	Depth	-0.018	0.97
	Hangar v South	0.021	0.16
	Hangar v Anchorage	0.013	0.24
	South v Anchorage	0.021	0.14

Seasonality of occurrence

Because no clear patterns of spatial distribution were detected, samples from all locations and both depths were pooled by month for analyses of seasonality. The two years of the study (2001, 2002-3), however, were analysed separately to enable comparison between them.

Larvae of benthic invertebrates were present in the water column in every month of the year. Most taxa, however, were seasonal in occurrence and those which were present throughout the year generally showed distinct seasonal maxima. An MDS ordination of Bray-Curtis similarities between larval assemblages averaged across all samples in each month of the study (Figure 9.4) indicated an annual cyclicity through the year 2002-3 (RELATE correlation with an idealised cyclical matrix: $\rho = 0.97$, $P < 0.001$), and that this pattern repeated in successive years of the study (assemblages in March 2001, March 2002, and February 2003 were more similar to each other than to assemblages at any other time through the study). This ordination also indicates that there was less variability between larval assemblages in successive months during the winter (May – September) than at other times of the year, and that similarity between the two successive years was greatest in this period.

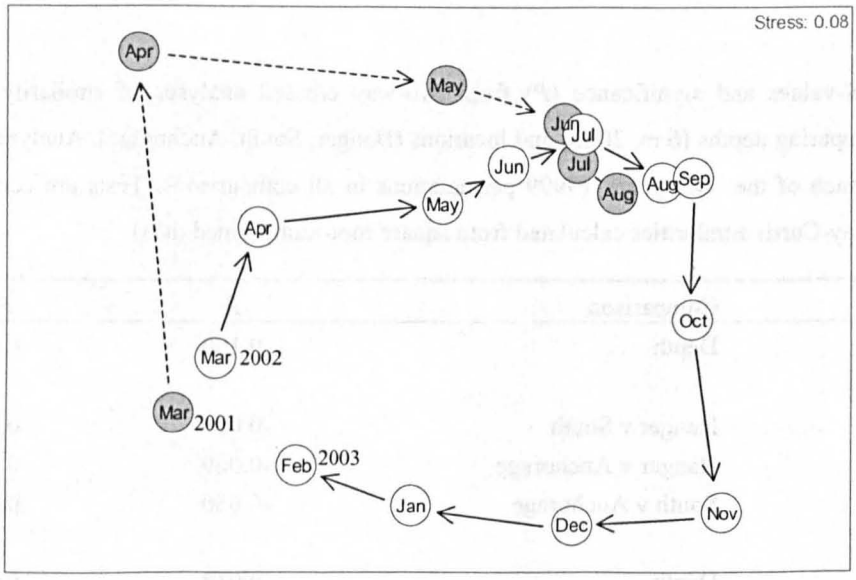


Figure 9.4 MDS ordination of Bray-Curtis similarities between assemblages of invertebrate larvae sampled in successive years: March - August 2001 (grey symbols), and March 2002 – February 2003 (open symbols). Plots represent the average assemblage in each month pooled across 2 depths (6 m and 20 m) and 3 locations (Hangar Cove, South Cove, and Anchorage).

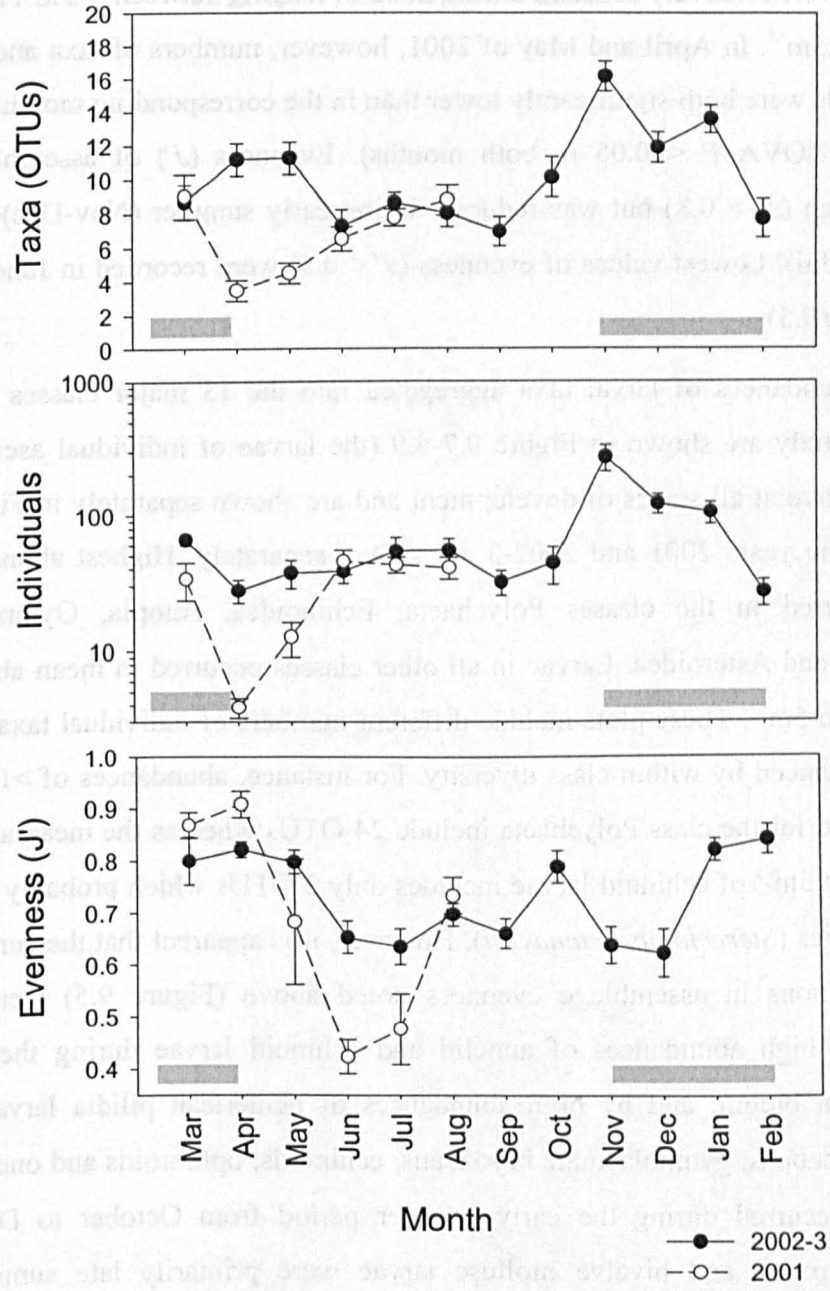


Figure 9.5 Total number of larval taxa, total number of larval individuals, and overall sample evenness (Pielou's *J'*) in the two years of the study. Values are standardised to 5 m^3 sample volume and are means of n = 6 samples in 2001, and n = 12 samples in 2002-3, error terms 1SE. Grey bars indicate the approximate duration of the summer phytoplankton bloom. (Note log scale for abundances).

The total number of taxa and the total number of individuals were highest in summer (Nov-Jan) and peaked in November (16.2 ± 0.9 taxa $5m^{-3}$, 272 ± 61 inds.$5m^{-3}$, Figure 9.5). Outside of the summer bloom period, mean numbers of larval taxa and

individuals were relatively constant during 2002-3, ranging between 7 and 11 taxa, and ~30-50 inds.5m^{-3}. In April and May of 2001, however, numbers of taxa and numbers of individuals were both significantly lower than in the corresponding months of 2002-3 (1-way ANOVA $P < 0.05$ in both months). Evenness (J') of assemblages was generally high ($J' > 0.8$) but was reduced during early summer (Nov-Dec) and mid-winter (Jun-Jul). Lowest values of evenness ($J' < 0.5$) were recorded in June and July 2001 (Figure 9.5).

Seasonal abundances of larval taxa aggregated into the 13 major classes identified during the study are shown in Figure 9.7-9.9 (the larvae of individual ascidian taxa were distinctive at all stages of development and are shown separately in Figure 9.6). Data from the years 2001 and 2002-3 are shown separately. Highest abundances of larvae occurred in the classes Polychaeta, Echinoidea, Anopla, Gymnolaemata, Gastropoda, and Asteroidea. Larvae in all other classes occurred in mean abundances of <10 larvae 5m^{-3}. These plots include different numbers of individual taxa and thus may be influenced by within-class diversity. For instance, abundances of >120 larvae 5m^{-3} recorded for the class Polychaeta include 24 OTUs whereas the mean abundance of >70 larvae 5m^{-3} of echinoid larvae includes only 2 OTUs which probably represent a single species (*Sterechinus neumayeri*). However, it is apparent that the summer and winter reductions in assemblage evenness noted above (Figure 9.5) were caused primarily by high abundances of annelid and echinoid larvae during the summer phytoplankton bloom, and by high abundances of nemertean pilidia larvae during winter. Anthozoans, gymnolaemate bryozoans, echinoids, ophiuroids and one ascidian taxon also occurred during the early summer period from October to December, whereas gastropod and bivalve mollusc larvae were primarily late summer taxa (January to April). Asteroid larvae were abundant through the latter part of the winter (July to November) and a clear progression of developmental stages indicated that the majority of these larvae represented a single taxon; this is presumably the most abundant asteroid species in the area, *Odontaster validus*. Sponge, hydrozoan, and holothurian larvae occurred in low abundances (<4 larvae 5m^{-3}) and with no clear seasonality. Despite strong seasonality of maximum abundances in the classes Anopla and Polychaeta, these taxa also occurred throughout the year at lower abundance.

Values of the ubiquity index Ub_{max}, averaged across all OTUs in each class, are shown beside each plot in Figures 9.6-9.9. These indicate how uniformly distributed each taxon was across the study sites. The highest mean ubiquity values ($Ub_{max} > 0.6$) were those of nemerteans (class Anopla), the ascidian morphotype 1 (Taxon 42), echinoids, and asteroids. Polychaete and bryozoan larvae, by contrast, were more unevenly distributed ($Ub_{max} \sim 0.5$) despite high mean abundances. Ophiuroids and gastropods also showed intermediate values of ubiquity (~0.5) but the remaining classes and taxa occurred only very patchily ($Ub_{max} < 0.4$).

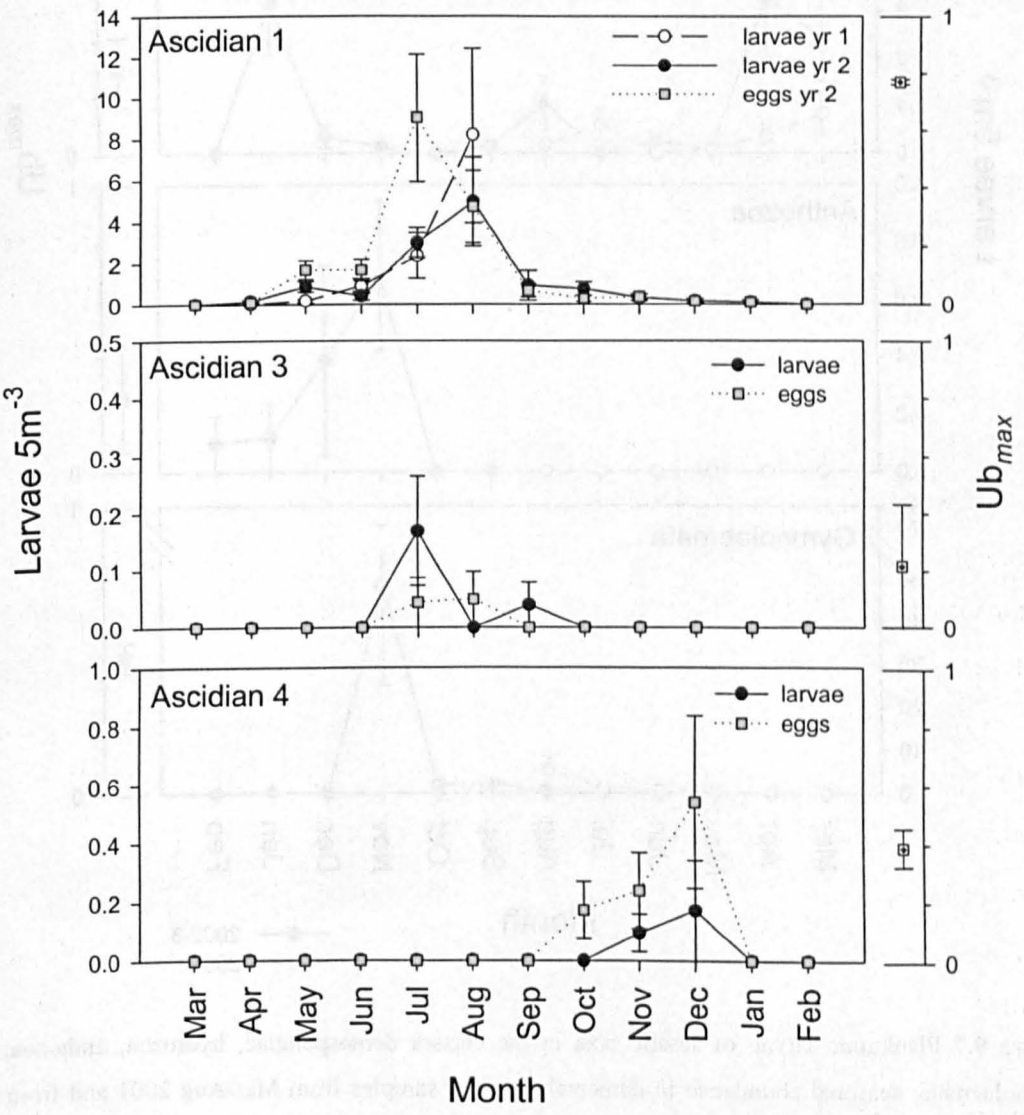


Figure 9.6 Ascidians: seasonal abundance of planktonic larvae and eggs of 3 morphotypes from Mar-Aug 2001 (yr 1) and from Mar 2002 to Feb 2003 (yr 2). Values are standardised to $5m^3$ sample volume, plots show means ± 1SE. The ubiquity index Ub_{max} (right) is averaged across all OTUs in each taxon.

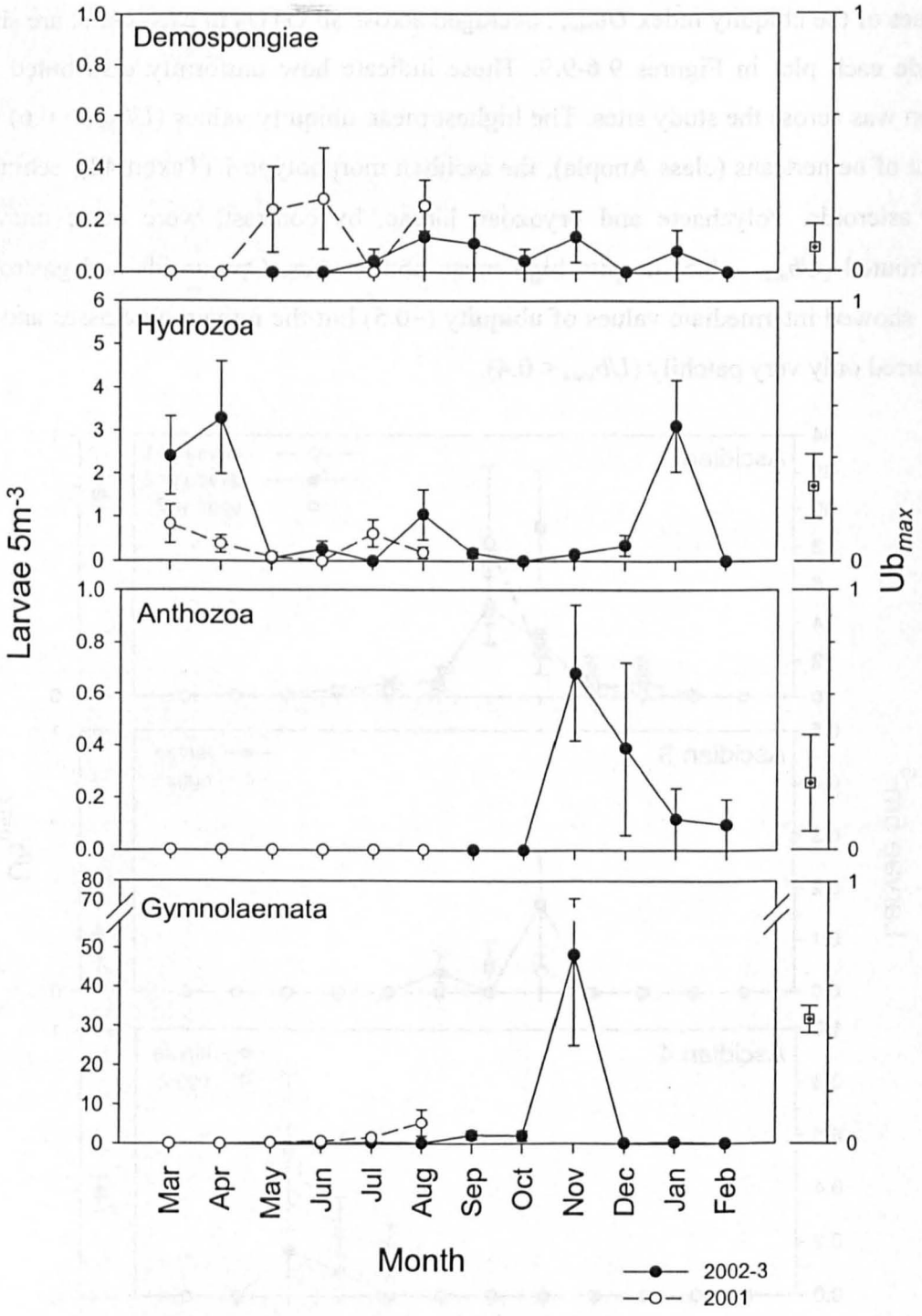


Figure 9.7 Planktonic larvae of sessile taxa in the classes demospongiae, hydrozoa, anthozoa, and gymnolaemata: seasonal abundance in demersal plankton samples from Mar-Aug 2001 and from Mar 2002 to Feb 2003. Values are standardised to $5m^3$ sample volume, plots show means ± 1SE. The ubiquity index Ub_{max} (right) is averaged across all OTUs in each class (for *n* see Table 1), error terms 1SE.

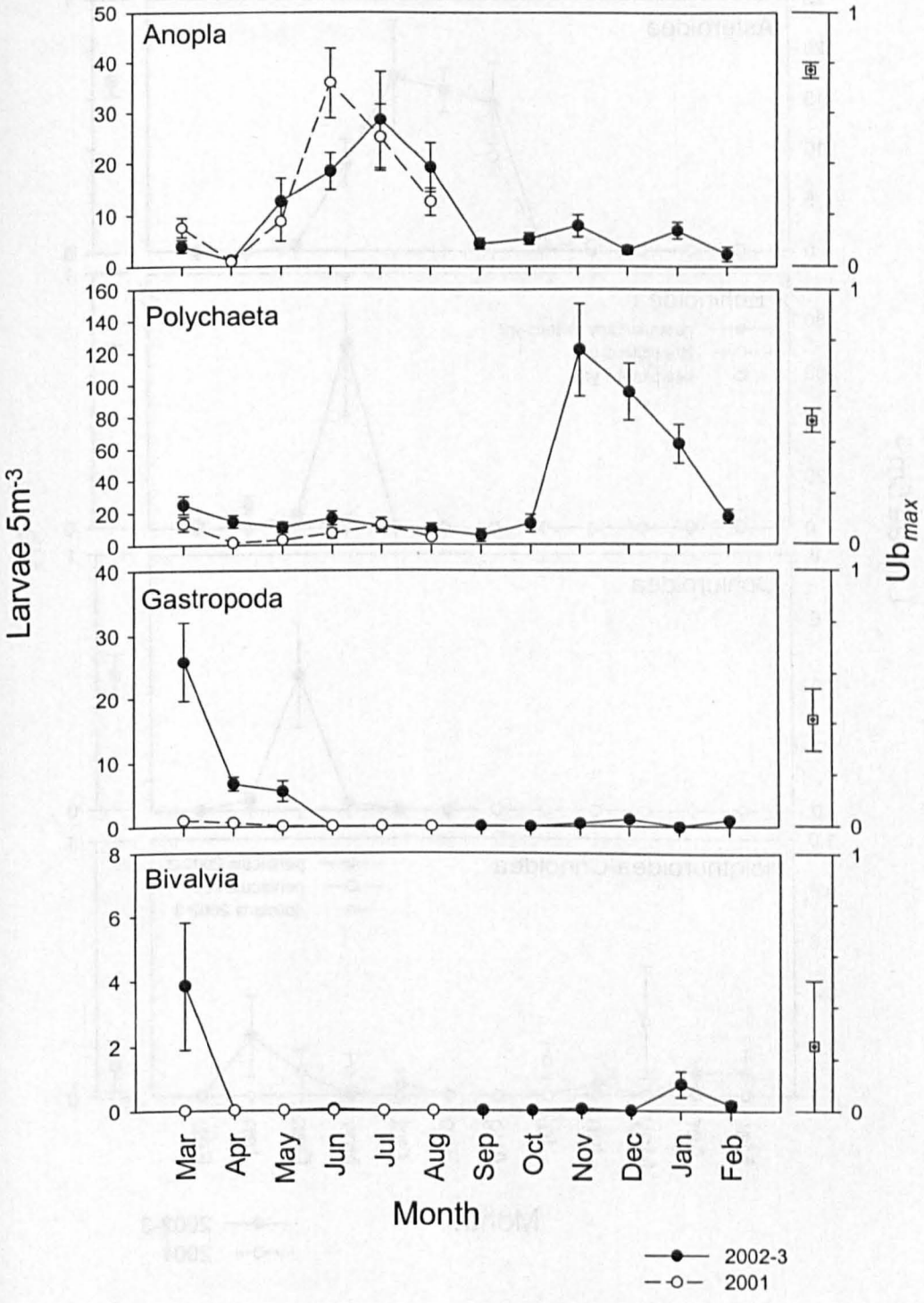


Figure 9.8 Anopla, Polychaeta, Gastropoda, and Bivalvia: seasonal abundance of planktonic larvae from Mar-Aug 2001 and from Mar 2002 to Feb 2003. Details as for Figure 9.7.

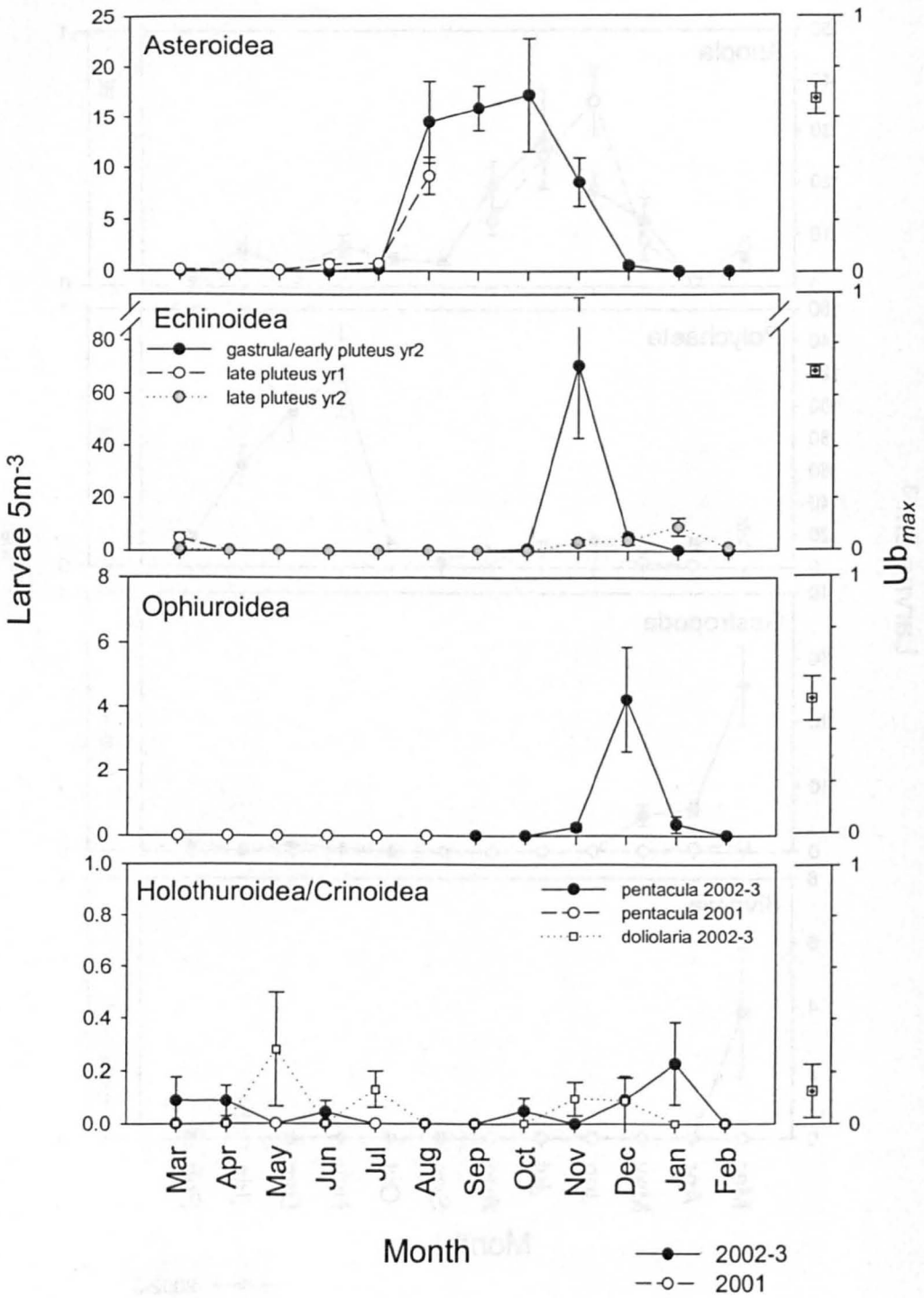


Figure 9.9 Echinodermata: seasonal abundance of planktonic larvae in the classes Asteroidea, Echinoidea, Ophiuroidea, Holothuroidea and Crinoidea from Mar-Aug 2001 and from Mar 2002 to Feb 2003. Doliolaria larvae (lower panel) are present in both holothurian and crinoid life cycles and these classes cannot be distinguished here. Details as for Figure 9.7.

DISCUSSION

Diversity

Stanwell-Smith et al. (1999) concluded that the number of marine invertebrate species producing pelagic (planktonic) larvae at Signy Island in the maritime Antarctic was in the range of 100-150 species, and that this was broadly comparable with the number (~160) found by Thorson (1946) in Danish waters. The estimated total of 99 benthic species producing planktonic larvae in the present study is lower than either of these but there are strong similarities between the data from Signy and the present study. Indeed, the great majority of taxa described by Stanwell-Smith et al. (1997) were also found here and a comparison of records from both surveys suggests that most of the difference between OTU totals can be explained by decisions made regarding the inclusion or aggregation of taxa. The availability of more comprehensive literature (e.g. Young 2002), and particularly the application of digital photographic techniques for the retrospective comparison of specimens from different months or years, have enabled successive developmental stages to be linked more reliably in the present study. In light of this, the present data do not suggest any clear difference in the numbers of taxa reproducing by planktonic larvae at Signy Island and at Adelaide Island.

Broad comparisons of data from these two Antarctic studies with Thorson's (1946) study in Denmark suggest that annelid larvae and echinoderm larvae contribute very similar proportions to total meroplankton assemblages at all three locations but that there are considerably fewer molluscan larvae in the Antarctic (Table 9.4). Furthermore, while the proportions of annelids and echinoderms in both Antarctic studies are similar (suggesting that any differences are not related to biases introduced during identification), there is a pronounced decrease in the proportion of molluscan larval taxa in the present study compared with Signy. Molluscs are the group on which Thorson (1950) based his original conclusion of a cline of decreasing incidence of planktonic larvae with increasing latitude, and the low numbers of molluscan larvae recorded here may be an expression of such a cline. However, the diversity of planktonic, planktotrophic, larvae from other phyla in the present study and elsewhere in the Antarctic (Bosch & Pearse 1990, Pearse et al. 1991b, Stanwell-Smith et al. 1999, Sewell 2005) suggests that the factors underlying such a cline are unlikely to be related

to the scarcity of planktonic food as postulated by Thorson (1950). For gastropods around the Chilean and Argentinean coasts of South America, Gallardo & Penchaszadch (2001) concluded that phylogenetic constraints in taxa associated with different types of substrata were more important predictors of reproductive mode than was latitude. The substratum at one of the two principal sampling locations in the Signy Island study was soft-sediment (Billies Rock, Stanwell-Smith et al. 1999) and the authors noted greater abundance of molluscan veligers at this site. It is possible, therefore, that lower molluscan larval abundance in the present study is a consequence of local habitat type rather than latitude *per se*. Furthermore, considerable variability in the abundance of planktonic larvae of gastropods was recorded over 3 summers at King George Island (62° S, 58° W) (Absher et al. 2003), which suggests that inter-annual variability could also have a strong influence on the observed differences between studies.

Table 9.4 Annelida, Mollusca, and Echinodermata: number of OTUs per phylum and % contribution to total meroplankton assemblages at Adelaide Island (present study), Signy Island (Stanwell-Smith et al. 1999, and Øresund (Thorson 1946).

	Annelida	Mollusca	Echinodermata
Øresund	41 (26%)	77 (48%)	16 (10%)
Signy Island	36 (27%)	30 (23%)	18 (14%)
Adelaide Island	24 (24%)	11 (11%)	11 (11%)

Abundance

While the taxonomic diversity of meroplanktonic larvae shows some broad similarities across studies, overall abundances differ considerably. In the present study the maximum mean monthly abundance of planktonic larvae was 272 ± 61 inds.5m^{-3} (Nov 2002, Figure 9.5). This is an order of magnitude higher than recorded by Stanwell-Smith et al. (1999) at Signy Island (maximum mean monthly abundance, across all taxa, 13.7 individuals.5m^{-3}), by Sewell (2005) in McMurdo Sound (~45 inds.5m^{-3} during November-December), and by Shreeve & Peck (1995) at offshore sites in the Bellingshausen sea (<10 inds. 5m^{-3} during November-December).

Comparisons with Sewell (2005) and Shreeve & Peck (1995) are compromised by differences in methodology but the Signy study is directly comparable in terms of both sampling and analysis protocols. It is of note, however, that the patchy distributions of

presumably short-duration larvae can cause large variations in abundances within months. In the present study, the highest larval abundance in a single tow was 637 larvae.$5m^{-3}$ at 6m depth in Hangar Cove during November, but only two other samples during the whole study yielded abundance values >500 larvae.$5m^{-3}$. These high abundances were due almost entirely to echinoid gastrulae and coronate bryozoan larvae (presumably *Sterechinus neumayeri* and *Fenestrulina rugula* respectively) and although adult populations of these species were present at Signy, they were far less abundant there than in the present study area (Barnes 1995c). Echinoid larvae are planktotrophic and generally well-dispersed in the water-column ($Ub_{max} > 0.6$) but bryozoan coronates are short-term, lecithotropic, larvae with pronounced swimming behaviours (Ryland 1960) which contribute to patchy planktonic distributions ($Ub_{max} < 0.5$). Comparisons of overall mean abundances, therefore, may be strongly influenced by high abundances of larvae of locally dominant taxa, the populations of which may be patchy on a local scale, thus distorting any broader, latitudinal or oceanographic patterns.

Despite this, mean monthly abundances through the remainder of the year in the present study ranged between 30–80 inds.$5m^{-3}$ and thus were still more than double the maximum value at Signy. Stanwell-Smith et al. (1999) hypothesised that the low larval abundances they recorded were a consequence of dilution resulting from extended larval durations at low temperature (Bosch et al. 1987, Peck 1993), and the oceanic location of Signy Island. Extended larval development times allow greater potential for planktonic larvae to be dispersed in the water-column and, in a relatively isolated oceanic context swept by the Antarctic Circumpolar Current, there may be considerable off-shore advection of larvae at Signy. In the absence of upstream source populations, such offshore transport might be expected to result in low larval abundances (Bhaud & Duchene 1996). In contrast to this, the present study was conducted at a continental location where currents are predominantly generated by a semi-diurnal tidal regime (data from Proudman Oceanographic Laboratory). Within Ryder Bay (Anchorage and South Cove sites) this generates oscillatory currents and in Hangar Cove currents are negligible (personal observation). Offshore advection of larvae, therefore, is unlikely to be significant. Furthermore, although relatively few sublittoral sites have been explored in the region so far, hard substrata predominate throughout the eastern margins of Marguerite Bay and it is likely that benthic

assemblages similar to those at the study sites are widespread. Thus, any net advection of larvae away from a given site will be compensated by immigration from neighbouring populations. Any effects of dilution, therefore, are unlikely to be as pronounced as at Signy Island. These factors, rather than any major difference in the taxonomic composition of assemblages, may account for the greater abundances of planktonic larvae recorded here.

Common to both the present study and the Signy Island study is the prevalence of larval stages of vagile, as opposed to sessile, taxa. Highest abundances of planktonic larvae were recorded in the classes Polychaeta, Echinoidea, Anopla, Gymnolaemata, Gastropoda, and Asteroidea. Of these, only one class, the Gymnolaemata, represents an entirely sessile group. Although the Polychaeta includes the families Spirobidae, Serpulidae, and Sabellariidae, which are sessile when adult, the majority of polychaete larvae recorded were those of errant worms, particularly spionids, syllids, and polynoids. Thus, the great majority of planktonic larvae recorded during this study were of vagile taxa and, with the exception of the Gymnolaemata, larvae of sessile taxa were present in low numbers. Planktonic larvae of vagile taxa were also more evenly distributed in the water column, as evidenced by higher average values of the ubiquity index Ub_{max} (Ub_{max} vagile > Ub_{max} sessile, Mann-Whitney U test $P < 0.05$). Although this study was not expressly designed to measure dispersal distances, Ub_{max} can, arguably, be interpreted as a proxy measure of relative planktonic duration. Thus, these data indicate generally greater dispersal distances in larvae of vagile taxa than of sessile taxa. An exception to this general pattern is the ascidian recorded here as Ascidian 1, the larvae and eggs of which are only moderately abundant but very evenly dispersed across the study area ($Ub_{max} > 0.7$). Judging by the coloration of larvae and early recruits, and by their abundance in relation to other ascidian larvae, it seems probable that this species is *Cnemidocarpa verrucossa*. This species is widespread and locally very abundant along the Antarctic Peninsula, and exhibits relatively rapid growth (Rauschert 1991, Tatian et al. 1998, Sahade et al. 2004). It is significant to the present discussion, however, that it is a solitary species, which might suggest that the distinction between unitary and modular organisation in sessile taxa may also be relevant to reproductive mode.

The observation that modular sessile marine taxa tend to reproduce via lecithotropic larvae of short planktonic duration (and therefore short dispersal distance) is not new. Jackson (1986) has suggested that short dispersal in these taxa confers advantages in terms of reproductive success and the pre-emption of substratum space through merging of genetically related colonies. In the context of near-shore Antarctic habitats, however, the differing strategies of vagile and sessile benthos appear paradoxical. Frequent disturbance by iceberg impacts is characteristic of these habitats and, for sessile taxa in particular, dispersal during the larval phase would appear to be essential to avoid local extinction. However, the obvious success of sessile fauna in the Antarctic suggests a need to consider the finer detail of dispersal strategies in relation to disturbance regimes. Thus, not only the scale of dispersal in relation to the typical patch size of disturbance, but also integrated dispersal distances over consecutive generations between disturbance events in a given patch, and the effect of 'rare' longer-distance dispersers in spawnings of otherwise locally-recruiting larvae may have significant effects on distributions.

Seasonality and larval type

Planktonic larvae were present in the water-column throughout the year. The majority of individual taxa, however, were strongly seasonal in occurrence and a range of larval timings is apparent (Figure 9.7-9.9). For all taxa in which comparable data are available from Signy Island (Stanwell-Smith et al. 1999), Ellis Fjord (Kirkwood 1994), and McMurdo Sound (Pearse 1965, Bosch et al. 1987), the periods of maximum abundance match closely those recorded in the present study, suggesting that these timings are general across regions and years. From an ecological perspective, however, the data suggest few clear patterns to support simple predictions as to the selective advantages of different developmental modes: planktotrophic larvae are abundant not only during the summer bloom but also throughout the winter (nemerteans and asteroids); lecithotropic and planktotrophic larvae occur simultaneously at all times of year (e.g. gymnolaemate bryozoans, echinoids), and pelagic durations of planktotrophic larvae may be either extended (e.g. asteroids, nemerteans) or brief (e.g. echinoids, ophiuroids, polychaetes).

The conspicuous winter peaks of abundance of planktotrophic nemertean and asteroid larvae contrast strongly with the timing of the summer bloom and are apparently

paradoxical as all larvae in these groups were planktotrophic forms (pilidia and bipinnaria). Winter spawning in the nemertean *Parbolasia corrugatus* and the asteroid *Odontaster validus* has been documented previously (Pearse 1966, Peck 1993, Stanwell-Smith & Clarke 1998a) and, considering their high population densities in the study area (Chapter 3), it is likely that the majority of the nemertean and asteroid larvae recorded here belong to these species. Larvae of both species have been shown to feed on bacteria, nanoplanktonic primary production, and perhaps dissolved organic matter during development (Rivkin et al. 1986, Bosch & Rivkin 1988, Peck 1993, Shilling & Bosch 1994) and thus are not solely dependent on the main phytoplankton bloom. However, while this provides a mechanistic explanation of how they persist through the winter, it does not explain the adaptive, ecological, pressures underlying a strategy of winter spawning.

Although the winter-occurring planktotrophic larvae of these species are of considerable interest, it is important to note that they are exceptions, and that the majority of planktonic larvae, both planktotrophic and lecithotropic, occurred during summer: in echinoids, ophiuroids, molluscs, anthozoans, and most polychaetes, the period of maximum abundance coincided with the summer bloom. This suggests that the timing of larval release in the majority of taxa with planktonic larvae is coupled to the seasonal pulse of primary productivity, as might be predicted for planktotrophic, but not necessarily lecithotropic larvae (Thorson 1950, Olson et al. 1987, Clarke 1992). It is of particular interest here, however, that the larval period of asteroids ends in December. Thus, following winter spawning and pelagic, planktotrophic, development, metamorphosis and settlement in this taxon coincides with the beginning of the summer bloom (Figure 9.9, top panel). Furthermore, the other winter-spawning taxon with planktotrophic larvae, the nemerteans, were observed to metamorphose and separate from their pilidia only in summer. This is apparent in the summer peak in abundance of juvenile nemertean worms recorded in the plankton samples (Figure 9.10, top panel). Metamorphosis of nemerteans has also been observed at this time of year in samples from the Bellingshausen Sea (Shreeve & Peck 1995) and Signy Island (Stanwell-Smith et al. 1997), suggesting that this is a general pattern. Thus, despite a conspicuous mid-winter peak of larval abundance, and year-round presence in the water-column, nemertean larvae also evidently metamorphose and settle to the benthos at the time of maximum phytoplankton availability.

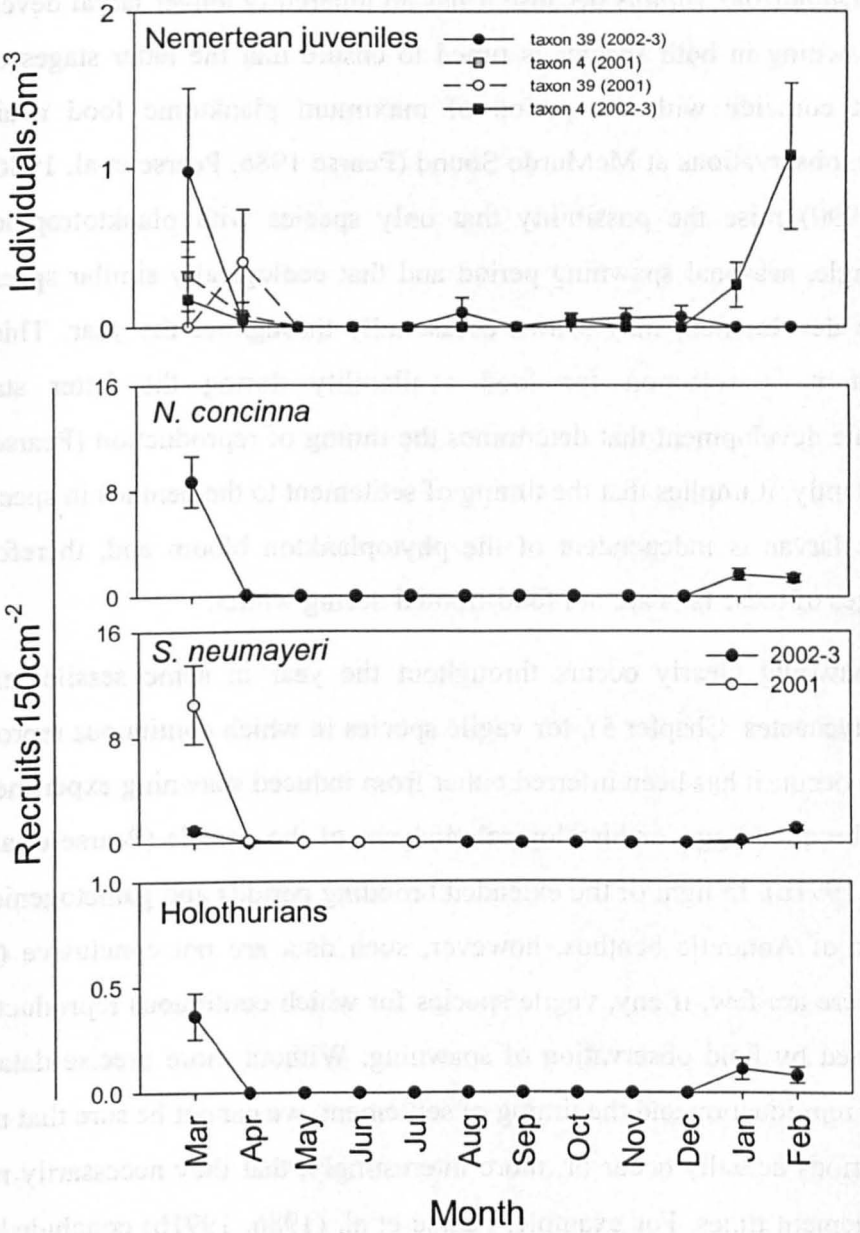


Figure 9.10 Seasonality of occurrence of post-metamorphosis juveniles of vagile benthic taxa. Top panel; nemertean worms (class Anopla) in demersal plankton samples. Lower panels; *Nacella concinna, Sterechinus neumayeri,* and holothurians recruiting to settlement panels immersed at monthly intervals. Black-filled symbols show abundances during 2002-3, open and grey-filled symbols show 2001 data. For *N. concinna* and holothurians no data are available for 2001.

Pearse (1965) suggested that the range of spawning seasons exhibited by Antarctic species with planktotrophic larval development is a consequence of interspecific differences in rates of embryonic and larval development in relation to the feeding requirements of the later larval stages. Thus, *Parborlasia corrugatus* spawns earlier in

winter than *Odontaster validus* because it has an inherently longer larval development time and spawning in both species is timed to ensure that the latter stages of larval development coincide with the period of maximum planktonic food availability. Furthermore, observations at McMurdo Sound (Pearse 1986, Pearse et al. 1986, Bosch & Pearse 1990) raise the possibility that only species with planktotrophic larvae exhibit a single, seasonal spawning period and that ecologically similar species with lecithotropic development may spawn aseasonally throughout the year. This would suggest that it is selection for food availability during the latter stages of planktotrophic development that determines the timing of reproduction (Pearse 1965). More importantly, it implies that the timing of settlement to the benthos in species with lecithotropic larvae is independent of the phytoplankton bloom and, therefore, that juvenile stages of these taxa are not food-limited during winter.

Although spawning clearly occurs throughout the year in some sessile taxa (e.g. spirorbid polychaetes, Chapter 5), for vagile species in which continuous reproduction is thought to occur, it has been inferred either from induced spawning experiments, the presence of brooded eggs, or histological analyses of the gonads (Pearse et al. 1986, Pearse et al. 1991b). In light of the extended brooding periods and gametogenic cycles characteristic of Antarctic benthos, however, such data are not conclusive (Arnaud 1977) and there are few, if any, vagile species for which continuous reproduction has been confirmed by field observation of spawning. Without more precise data on the frequency of reproduction and the timing of settlement, we cannot be sure that multiple spawning periods actually occur or, more interestingly, that they necessarily result in multiple settlement times. For example, Pearse et al. (1986, 1991b) concluded that *P. corrugatus* probably spawned continuously throughout the year, based largely on gonadal smears and the presence of larvae in the water column. Recent data from a long-term study of reproductive cycles of marine invertebrates at Rothera, however, indicate that *P. corrugatus* spawns annually with consistent timing between years (1997-2001) despite the presence of large oocytes throughout the study (L. Grange, Southampton Oceanographic Centre, pers comm). The present data also suggest a pattern of seasonal reproduction in late-summer to early-winter for this species, followed by an extended larval period with metamorphosis and settlement in summer (Figure 9.8 & 9.10). Thus, the inference of continuous, aseasonal spawning from the

presence of large oocytes in the gonads, or of larvae in the water column, is questionable.

An alternative interpretation of the patterns of larval duration and settlement in the present study is that reproduction is timed to maximise food availability, not for the larva, but for the settling juvenile. Arnaud (1977) suggested that such a strategy may be general amongst Antarctic ectotherms. He speculated that both the timing of settlement and the timing of the initiation of gametogenesis are determined by the availability of food for the settling juvenile and for the adult respectively. This was based on observations that both settlement and the onset of gametogenesis take place during the period of the summer phytoplankton bloom. Selection for an optimal time of settlement, rather than an optimal period for larval feeding, has also been proposed by Todd & Doyle (1981) to explain differences in the spawning times of ecologically similar species with different larval durations. Using the example of temperate latitude nudibranch molluscs, these authors proposed that where an optimal time for the adult to spawn and an optimal time for the larva to settle are separated, there would be selection for a larval duration which most effectively spans the intervening period. Significantly, Todd & Doyle (1981) noted that if the requirements of adult and juvenile are different, selection might be stronger for either the time of spawning, or the time of settlement. Thus, if juveniles depend on a specific temporally limited type or size of food but spawning time in adults is not constrained by seasonal food availability, it is the timing of settlement which will be most strongly selected for.

The initiation of spawning can be triggered by a variety of external and internal cues (Starr et al. 1990, Morgan 1995b) but is dependent on the completion of gametogenic cycles. These are influenced by nutritional status and thus might be expected to be seasonal. Oogenesis, in particular, is energetically expensive and might be expected to have a limiting influence on the frequency and timing of reproduction. Oogenesis in many Antarctic invertebrates is not annual but takes place over 1.5-2 yr cycles (Pearse 1965, Brockington 2001a, Powell 2001, Tyler et al. 2003, Grange et al. 2004). These slow rates of development are thought to be a physiological consequence of low temperature *per se* (Hoegh-Guldberg & Pearse 1995) although food-limitation, and larger egg size as an adaptation to development in cold water with seasonal food input (Clarke 1982, 1992) have been suggested as alternative, or contributory, factors.

Regardless of the underlying causes, however, extended oogenesis may also have an important ecological effect in that it allows fluctuations in food availability to be integrated over more than one annual cycle (Arnaud 1977, Clarke 1992). Thus, the time of spawning is, to some extent, decoupled from seasonal food availability. The Antarctic scallop *Adamussium colbecki* is an exception to this pattern in that gametogenesis follows an annual cycle with spawning in late September to early October. Oogenesis in this species thus takes place largely during winter and is probably fuelled by energy stored in the digestive gland (Tyler et al. 2003). There are, therefore, at least two mechanisms (extended gametogenesis and energy storage) by which the time of spawning can be decoupled from immediate dependence on the period of maximum food availability. Thus, for many taxa, neither larval type nor the timing of spawning appear to be directly constrained by the timing of the summer bloom. This suggests that the timing of settlement may be the single most important criterion in the life cycle.

Settlement timing in relation to adult trophic mode

The lower three panels in Figure 10 show the mean abundances of post-metamorphosis juveniles of limpets (*Nacella concinna*), urchins (*Sterechinus neumayeri*), and holothurians (probably *Ekmocuminis steineni*) settling to acrylic panels during the period of the larval survey (data recorded during the short-term recruitment study, Chapter 5). These taxa feed primarily on benthic algal films and phytoplankton settling to the seabed (Brand 1980, Barnes & Clarke 1995, Brockington et al. 2001, Fraser et al. 2002a). In each taxon, recruitment is restricted to the period of the summer bloom but larval durations (as deduced from the seasonal abundance plots, Figure 9.7-9.9) are considerably shorter than for nemerteans or asteroids. All three spawn during summer, *S. neumayeri* producing planktotrophic larvae and the most common holothurian, *Ekmocucumis steineni*, producing lecithotropic larvae (Bosch et al. 1987, Gutt et al. 1992, Stanwell-Smith & Clarke 1998b, Stanwell-Smith & Peck 1998). *N. concinna* forms pelagic veligers but it is uncertain whether they feed or not (Stanwell-Smith & Clarke 1998b). Thus, these species have similar food requirements and settlement is constrained to summer, possibly because juveniles are dependent on seasonally available benthic algal films and phytoplankton deposits.

Settlement of nemerteans and asteroids here (presumably, most of these are *Parborlasia corrugatus* and *Odontaster validus*) also occurs during the summer bloom. However, there are conspicuous differences in life history in that spawning takes place in winter and adult diet is primarily carnivorous. Although *O. validus* consumes deposited and suspended phytoplankton during summer, this species and *P. corrugatus* are both opportunist predators and scavengers and are often seen consuming other fauna during winter (Pearse 1965, Dayton et al. 1974, Dearborn 1977, and per. obs.). Therefore, food is potentially available throughout the winter and is not dependent directly on the summer phytoplankton input. Post-metamorphosis juveniles of these species, however, are small (~1 mm at settlement, personal observation) and are, therefore, likely to be dependent on the juveniles of other benthic taxa as prey. As the majority of potential prey taxa recruit to the seabed in summer, there may be selective pressure for the juveniles of these predatory taxa to settle at the same time. Both *P. corrugatus* and O. *validus* have planktotrophic larvae but other omnivorous and carnivorous species with different developmental strategies also settle during summer. For instance, the carnivorous mollusc *Marseniopsis mollis* (Peck et al. in prep) and the opisthobranch *Piline gibba* (Seager 1979) spawn in late summer, develop through winter in protected brood cases, hatch as either late-development veligers (*M. mollis*) or non-feeding juveniles (*P. gibba*) and commence feeding in mid to late summer (Figure 9.11).

Thus, across a range of taxa with widely differing reproductive strategies and spawning times, settlement occurs during the period of the main summer phytoplankton bloom and this might be a consequence of food requirements of the juvenile. Adults of all of the taxa discussed above, however, including those reviewed by Arnaud (1977) and used by Todd & Doyle (1981) in the original formulation of the settlement-timing hypothesis, are vagile. Patterns of occurrence for larvae of sessile taxa in the present study are less consistent (Figure 9.6, Figure 9.7).

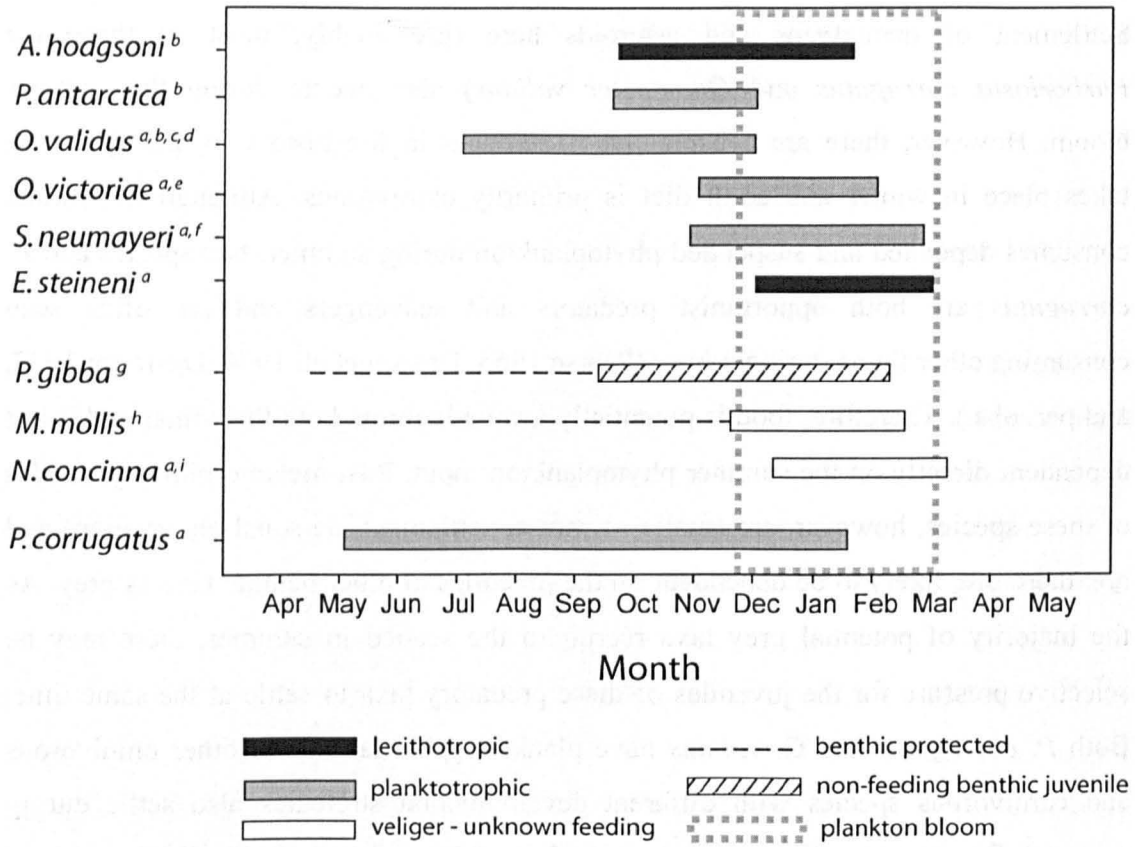


Figure 9.11 Larval development timings of 10 vagile species in relation to season. Bars show approximate durations of larval period from hatching to settling (left to right) and developmental mode (see legend). The boxed area (broad dotted line) indicates the period of the summer phytoplankton bloom. Sources: *a*, this study; *b*, Pearse et al. (1986) and Bosch (1989); *c*, Pearse (1965); *d*, Stanwell-Smith & Clarke (1998a), *e*, Grange et al. (2004); *f*, Bosch et al. (1984); *g*, Seager (1979); *h*, Peck et al. in prep; *i*, Stanwell-Smith & Clarke (1998b). Species: *Acondontaster hodgsoni, Porania antarctica, Odontaster validus, Ophionotus victoriae, Sterechinus neumayeri, Ekmocucumis steineni, Piline Gibba, Marseniopsis mollis, Nacella concinna, Parborlasia corrugatus.*

With the possible exception of larvae of some sessile polychaetes, which may be planktotrophic (Kupriyanova et al. 2001), and one bryozoan cyphonautes larva which may be teleplanic (Shreeve & Hayward 1995), all larvae of sessile taxa identified during this study were lecithotropic forms of short planktonic duration (Table 9.1, Figure 9.6, Figure 9.7). In contrast to the vagile groups, however, there is no single common period in which settlement occurs. One ascidian taxon occurred only in summer, sponge and hydrozoan planulae were present in most months of the year, bryozoan coronate larvae occurred from late winter to early summer, and two ascidian taxa occurred only in mid-winter. Furthermore, although pelagic anthozoan larvae

were recorded only in summer here, *Primnoella* sp. and *Alcyonium antarcticum* recruited to settlement plates in September-October and April-May, respectively (Chapters 5 & 6), and the short-term recruitment data overall show a late-winter peak in the numbers of sessile taxa settling to the benthos (Chapter 5). This range of settlement timings contrasts with the summer settlement of vagile taxa and might be explained in two ways. Firstly, planktotrophic larvae may be able to complete development only with the planktonic food available during the summer, whereas lecithotropic larvae can metamorphose in any season using stored reserves. Alternatively, differences between vagile and sessile taxa in feeding mode may select for different periods of recruitment.

As discussed above, post-metamorphosis recruits of most vagile taxa are obligate benthic feeders and are dependent for survival and growth on either the summer pulse of deposited phytoplankton, the growth of epilithic algal films, or on newly settled faunal prey. Sessile taxa, by contrast, are suspension feeders (Hughes 1989, Coma et al. 2001, Gili et al. 2001) and thus feed on planktonic material following settlement. The small size of food particles which can be utilised by post-metamorphosis juveniles in many of these taxa (see Chapter 5, discussion) is such that initial development might be able to proceed using the smallest nanoplanktonic fraction (2-20 μm) of primary production: this persists through much of the winter and commences earlier in spring than does the main bloom (RaTS data, Clarke & Leakey 1996). Thus, post-settlement juveniles of sessile taxa may not be dependent on the deposition of planktonic food. Settlement might, therefore, be decoupled from the summer bloom and selection for other aspects of life history may have greater influence on observed reproductive strategies.

Thorson's Rule

Although Thorson's Rule has been shown by recent investigations to be largely unsupported as a general rule (reviewed by Clarke 1992, Pearse 1994), it has not been replaced by any coherent ecological explanation of the observed patterns of reproduction in marine benthic invertebrates. It is appropriate, therefore, to consider how the present data relate to the original paradigm.

Two principal ecological assumptions underlie Thorson's conclusion that planktonic, planktotrophic, larvae are selected against in polar seas (Thorson 1950, Mileikovsky

1971). Firstly, he argued that the combination of a brief phytoplankton bloom and long development times would select against planktonic (planktotrophic) development in polar seas because of larval starvation. Secondly, extended larval development times would be unsupportable because of increased mortality from predation during the extended planktonic phase.

Several lines of evidence now suggest a modified view of the selective pressures acting to determine life-history strategies in polar benthic invertebrates. Firstly, at least two species produce planktotrophic larvae which feed and develop in the plankton during winter (Pearse 1969, Stanwell-Smith et al. 1999, this study). This argues against the assumption of food-limitation in the plankton. Secondly, these species are amongst the most abundant and widespread in the Antarctic nearshore ecosystem (Dayton et al. 1974, Kirkwood & Burton 1988, McClintock et al. 1988, Stanwell-Smith & Clarke 1998a, Bowden 2005). This argues against any appreciable limitation resulting from mortality in the plankton. Indeed, the plankton in winter may, arguably, be a safer and more constant environment than the benthos (Clarke 1992). Thirdly, settlement of these, and other vagile species, coincides with the summer phytoplankton bloom (this study). This, in combination with the first two points above, suggests that, for vagile taxa at least, selective pressures act more strongly on the immediate post-metamorphosis stage, and therefore on the timing of settlement, than on the larval phase. Finally, in species which release planktotrophic larvae in summer (e.g. *S. neumayeri*, *O. victoriae*), development to metamorphosis and settlement is completed by the end of summer. This undermines any argument that developmental times of planktotrophic larvae are too long, due to low metabolic rates at low temperature, to be completed during the short bloom.

Chapter 10 – General discussion

Chapter 10 – General discussion

Main findings of the study

This thesis describes four aspects of benthic assemblages in the study area: the spatial distribution of adult assemblages; the diversity, abundance and seasonality of recruitment; rates of growth and survivorship following initial recruitment, and the diversity, abundance, and seasonality of larvae in the water column. This is the first time that such a study has been completed within the Antarctic Circle and the data represent a considerable advance in spatial, temporal, and taxonomic resolution over previous studies. Moreover, in some important respects the present findings suggest a different picture of the processes underlying the distribution of benthic assemblages in nearshore Antarctic habitats than has previously prevailed. The principal findings can be summarised as follows:

- In each year that settlement plates were deployed, and across all locations, recruitment was abundant and the diversity of taxa recruiting was comparable to that in surrounding assemblages. This contrasts with the low levels of recruitment reported from previous Antarctic studies and suggests that recruitment limitation is not as important as post-settlement factors in the establishment of benthic assemblages in the study area.

- Subsequent development of sessile assemblages was highly variable at scales of m – km and between exposed and protected surfaces. Most of this variability was caused by biologically-mediated disturbance, particularly grazing by urchins. Thus, even at shallow depths, post-settlement biological interactions largely controlled assemblage development. This contrasts with the expectation that ice-mediated disturbance is the principal cause of mortality in Antarctic nearshore environments.

- Recruitment of sessile taxa took place throughout the year but taxon-specific recruitment periods were generally seasonal and a significant proportion recruited in winter, before the summer phytoplankton bloom. Comparable data are scarce but this appears to be in direct contrast to recruitment timings in temperate latitudes.

- Vagile taxa, by contrast, all recruited during the summer bloom, regardless of spawning time, larval type, or larval duration. This suggests that the characteristic of the larval phase which is most strongly selected for is the timing of settlement.

These points have been discussed in terms of underlying processes in the relevant chapters, and successive discussions have incorporated information from preceding chapters in a cumulative fashion. The present chapter, therefore, considers the main points from the data chapters in relation to the broader ecological questions raised in the general introduction.

Pre-settlement and post-settlement factors

Benthic assemblages in any habitat are likely to be structured by both pre-settlement factors (larval supply, e.g. Underwood & Fairweather 1989, Connolly & Roughgarden 1998) and post-settlement factors (competition, predation, environmental stress e.g. Paine 1969, Dayton 1971). However, the balance between these two sets of factors depends on the system under study and the temporal and spatial scales at which it is viewed (Caley et al. 1996). For instance, Dayton (1971) described an Antarctic sublittoral assemblage in terms of its maintenance by post-settlement interactions over a single year. The same assemblage however can apparently be strongly influenced by rare episodes of enhanced recruitment of key species (Dayton 1989). Similarly, on the Pacific coast of the USA, post-settlement interactions are important at smaller scales in short term studies (e.g. Paine 1969, Dayton 1971) but fluctuations in the recruitment of dominant taxa caused by large scale hydrographic processes play a significant role over longer time scales and larger areas (e.g. Connolly & Roughgarden 1998, Connolly et al. 2001).

Distinguishing between the relative influence of pre- and post-settlement factors can be problematic in many habitats (Caley et al. 1996) but, in others, ecological circumstances lead to a clear dominance by one or the other. In particular, where post-settlement mortality is consistently high it can mask fluctuations in recruitment. For instance, locally high population densities of predatory or grazing species can maintain sessile assemblages in a similar state over many years despite fluctuations in recruitment strength (Osman & Whitlatch 1998, Todd 1998, Osman & Whitlatch

2004). It seems likely that this may be the situation in the present study area. Although it is difficult to make absolute comparisons with other areas with respect to the diversity and abundance of settlement, the short-term recruitment data here (Chapter 5) show relatively abundant settlement at all sites throughout the year. Moreover, there was no appreciable difference in settlement between locations or to exposed upward facing and protected downward-facing surfaces. Subsequent patterns of assemblage development, particularly the very low levels of cover on the upper surfaces of all plates, indicate clearly that post-settlement mortality had a greater influence on assemblages than did recruitment limitation.

This is not to say that recruitment limitation plays no role in the observed distributions, however, as it is still possible that an increase in recruitment would result in increased survivorship if mortality is not strongly density-dependent (Caley et al. 1996). Furthermore, the lower diversity of fauna at Hangar Cove sites suggests that recruitment limitation through restricted dispersal ranges might play a role at larger scales (Chapter 1) and, as the present recruitment data span only one complete year, the influence of longer term fluctuations is impossible to assess. Indeed, in light of evidence that longer-term oceanographic cycles can cause significant interannual variability in Antarctic coastal habitats (Dayton 1989, Murphy et al. 1995, Meredith et al. 2004) it is, perhaps, unlikely that that there will not be variations in recruitment strength. At the scales studied here, however, post-settlement mortality was the overriding factor influencing assemblage development on most settlement plates. Grazing, by high densities of *Sterechinus neumayeri* and probably also by *Nacella concinna*, was the primary cause of mortality on exposed surfaces. At the deeper sites, biotic disturbance by a range of taxa affected survivorship on both upper and lower surfaces and was the most important cause of variability at all scales. Only at shallower depths (8m sites) did ice impacts have a significant effect.

The relative insignificance of ice-mediated disturbance to assemblages in this study is partly a consequence of site selection in that efforts were made to minimise the probability of damage. However, all plates were vulnerable to some extent (Figure 4.4) as demonstrated by the damage to plates at shallower sites. What is most interesting here is that, even at the shallow depths studied, habitat heterogeneity allows the existence of physical refugia which remain unaffected by ice for years. Thus, although

ice disturbance inevitably structures shallow water assemblages over longer time scales and larger spatial scales, biological interactions apparently play a greater role on exposed surfaces at shorter temporal scales, and within small-scale habitat refugia at all times.

Reproductive mode

The Antarctic marine environment imposes some fundamental limitations which probably apply to all taxa: seasonally limited primary production and the physiological effects of cold temperature, for instance, restrict rates of growth and development. However, data from this study and others around the continent show that many different life history strategies are apparently equally viable in the Antarctic nearshore environment. This observation should not, perhaps, be unexpected as there are few environments in which this is not the case. However, in light of the extreme seasonality of the Antarctic it might still be expected that there should be strong selection for some aspects of life history.

The life history characteristics of the present day fauna are likely to have been influenced by both historical and present selection pressures (see general introduction). This historical perspective is important to any discussion of life history strategies in the present Antarctic fauna and particularly to ideas of optimality in relation to developmental mode. Much previous discussion of life-history adaptations in Antarctic benthic invertebrates has centred on the significance of the different larval types in relation to the characteristics of the habitat (e.g. Thorson 1950, Clarke 1983, Pearse et al. 1991b, Clarke 1992, Pearse 1994, Stanwell-Smith et al. 1999). The main point to emerge from these discussions, however, is the inadequacy of hypotheses based purely on the selective pressures acting on the larval stage to explain the range of developmental strategies exhibited by benthic invertebrates in these waters (Pearse et al. 1991b, Pearse 1994). This suggests that such approaches might be searching for ecologically significant adaptations where none exist. More specifically, the co-occurrence of a broad range of larval feeding modes, planktonic durations, and reproductive timings in what appears to be a strongly selective physical environment suggests that larval mode itself is not a critical factor in benthic life cycles in the Antarctic.

The clearest distinction in the reproductive strategies of the taxa studied here is that between vagile and sessile taxa: the great majority of pelagic larvae are those of vagile taxa, whereas sessile taxa are poorly represented in the plankton (Chapter 9). However, this is a general pattern globally and is not peculiar to the Antarctic. Sessile organisms, particularly modular species, tend to have lecithotropic, short-dispersal larvae which settle close to the parent (Jackson 1986, Jackson & Coates 1986, Todd 1998). This may be an adaptation to facilitate the pre-emption of substrata or to increase the probability of fertilization success (Jackson 1986, this study chapter 6) but is unrelated to the specific circumstances of the Antarctic. Similarly, vagile taxa exhibit a broad range of developmental strategies in most habitats and the Antarctic is evidently not an exception. In some Antarctic taxa there is certainly an increase in the proportion of species reproducing via lecithotropic larvae (e.g. echinoids, holothurians, Pearse et al. 1991b, Pearse & Lockhart 2004) or brooding (e.g. gastropods, Picken 1980) by comparison with lower latitudes. However, if the present environment were to select strongly against planktotrophic development, reproduction via a purely planktotrophic larva in several of the most ecologically successful species (e.g. *S. neumayeri, O. validus, P. corrugatus, O. victoriae*) would be inexplicable.

It seems more plausible, therefore, that the relative occurrence of reproductive modes seen today may be largely the result of historical events (Clarke & Crame 1992, Poulin & Feral 1996, Poulin et al. 2002) and phylogenetic constraints (Strathmann 1985), rather than adaptation to the present day environment. If this is the case, the range of taxon-specific developmental modes present in the contemporary fauna is a complex mixture of adaptation to past conditions in some clades, ecological success in the present in others, and continuing adaptation to present conditions in all species. Despite the complexities inherent in this picture, however, we would still predict that each of these developmental modes should exhibit adaptations to the particular demands of present conditions in the Antarctic. Such adaptation may be evident in the timing of settlement.

Timing of settlement

In addition to the tendency for vagile and sessile taxa to have different larval types and durations, there are conspicuous differences in the timing of settlement between these groups: all vagile species for which reliable data are available settle during the period

of the summer bloom (Figure 9.11), whereas sessile species settle in all seasons and many settle in winter (Figure 5.9). The diverse range of developmental modes and spawning times exhibited by vagile species, all of which culminate in summer settlement, suggests that the timing of settlement is a more critical factor in the life cycles of vagile species than either larval type or duration.

Based on the settlement timings and larval durations here (Chapters 5 & 9) and in the literature, I suggest that the timing of settlement is affected primarily by selective pressures acting on taxon-specific food requirements of the juvenile. This is an idea that has previously been proposed to explain reproductive strategies in both temperate (Todd & Doyle 1981) and Antarctic (Arnaud 1977) benthic environments but other than a brief critical debate (e.g. Grant & Williamson 1985, Todd 1985) has since been largely ignored. In relation to the present data, this hypothesis is based on the argument that juveniles of grazers, predators, or coarse-particle suspension and deposit feeders, are dependent on seasonally available benthic food. This results in the necessity to settle during summer when large phytoplankton cells, benthic algal films, and the juveniles of prey species are available. Species that are able to feed on fine particulate suspended matter, by contrast, are not constrained to settle in summer because their juvenile stages feed on autotrophic nanoplankton cells which are present in the water column for all but ~2 months in winter (Figure 6.6). Because only sessile taxa are able to feed on such seston, a selective mechanism based on the feeding mode of the juvenile stage might account for the observed differences in settlement timing between vagile and sessile groups.

If the majority of sessile species are not constrained to settle during summer, the wide range of settlement timings they exhibit might be evidence that there is no generally applicable selective pressure affecting either the larval stage or the time of settlement. However, the short-term recruitment data (Chapter 5) show a trend for more taxa to recruit during winter than summer at 20 m, which contrasts with patterns in temperate regions (Figure 5.9). Highly seasonal summer feeding by the abundant deposit-feeding, coarse-suspension feeding, and grazing fauna is a striking characteristic of depths below ~15 m in the study area. It seems probable that such feeding causes increased mortality of settling larvae during the summer bloom and thus might exert a selective pressure for settlement outside of the main bloom. However, although the

winter settlement observed here is conspicuous, many sessile taxa still settle in summer, suggesting that the factors affecting settlement timing in sessile species are more complex. This is particularly apparent amongst encrusting bryozoan species (Figure 5.5). These species are likely to have very similar feeding requirements and can feed efficiently on nanoplankton at low concentrations (McKinney & Jackson 1989, Sanderson 1993) yet they exhibit a range of settlement timings from mid-winter to mid-summer. That their settlement timings are correlated with relative competitive ability is intriguing (see Chapter 5 discussion) but the factors underlying this pattern are difficult to interpret with the present data.

Disturbance & dispersal

The prevalence of short dispersal strategies in sessile taxa raises the question of how such taxa are able to persist in the Antarctic nearshore environment where disturbance by ice is frequent. In order to consider the influence of ice on the evolution of life history strategies in benthic organisms, however, it is necessary to differentiate between scales of disturbance. At one extreme, major disturbances result in complete defaunation over large areas (scales of >km^2). Such disturbances include the expansion of ice sheets over shallow shelf regions during glacial maxima and the grounding of the largest icebergs. These are, therefore, long term events lasting from years to thousands of years. At the opposite extreme, minor disturbances are caused by impacts of small to moderate size icebergs. Such impacts defaunate highly localised patches (cm^2 to m^2) and repeat on time scales from hours up to a few years with a frequency that is dependent on depth and topography. Thus, any conceptual model of succession dynamics in Antarctic benthic habitats faces the problem of two interacting disturbance gradients: a long-term, large-scale, temporal gradient of recolonisation following major disturbances, and a short-term, small-scale, spatial gradient of decreasing ice-scour with depth.

Minor disturbances are characteristic of shallow coastal waters (<~50m) during glacial minima, when much of the continental shelf is seasonally ice-free (as in the present). The icebergs which can affect these shallow habitats are necessarily small, because they are constrained by depth, and on hard substrata their impacts obliterate fauna only in localised patches. In such habitats, long distance dispersal would appear to confer no greater short-term advantage than do restricted dispersal strategies (Strathmann 1981,

1993). This is because the dispersal distances of long-lived planktonic larvae are likely to be significantly greater than the radius of disturbed patches. As long as realised dispersal distances approximate to the modal radius of disturbance patches, local extinction is unlikely. Furthermore, if disturbances occur at intervals of more than one year, it is the realised dispersal distance summed over the number of generations between disturbances on which selection will act. Thus, dispersal involves both spatial and temporal dimensions, and it is likely that there will be a continuum of potential strategies which ensure survival of the lineage under a given set of conditions.

It is also significant that recent modelling studies (e.g. Clark et al. 2001, Hill et al. 2002, Siegel et al. 2003, Davies et al. 2004, Kinlan et al. 2005) indicate that variability in dispersal range, both within species and within individual spawnings, can have important consequences for species distributions and survival. For sessile organisms, Clark et al (2001) have shown that leptokurtic "fat-tailed" distribution kernels, in which most offspring settle close to the parent but a small proportion disperse over significantly greater distances, simulate observed distributions and rates of colonisation more accurately than do conventional gaussian distribution kernels. For species with long-lived pelagic larvae, varying levels of local retention can result from topographically generated hydrodynamic characteristics in coastal (Kinlan et al. 2005) and oceanic (Mullineaux 1994) habitats. Thus, the concept of 'long' and 'short' dispersal strategies might be too crude to be useful in the context of the present, interglacial, disturbance regime.

Sessile species are dependent on substratum space for growth and reproduction, yet dispersal is of fundamental importance, even in undisturbed habitats (Hamilton & May 1977). In the context of the leptokurtic dispersal kernels described above (Clark et al. 2001) this suggests that the dispersal strategies of sessile fauna might be the result of a trade-off between two requirements: the need to consolidate substratum space, and the need to avoid local extinction resulting from competition or physical disturbance (Crowley & McLetchie 2002). The former can be achieved by high density of local settlement (see Chapter 6 discussion), into which the majority of reproductive effort is invested, while the latter is ensured by the small proportion of larvae which disperse further. From the discussion of dispersal distances in relation to disturbance size, disturbance frequency, and generation times above, and in light of the relatively small

size of patch disturbance characteristic of Antarctic nearshore environments, it may be that predominantly short dispersal (cm-m) combined with relatively rare longer range dispersal events is an evolutionarily stable strategy for survival in these habitats.

Differences in dispersal strategies of the common sessile and vagile taxa here have interesting implications for successional gradients following major disturbances such as the break-up of ice shelves or retreat of glaciers. When a large area of seabed becomes available for colonisation, the first colonists might be predicted to be opportunistic deposit-feeding and grazing taxa with widely-dispersing, planktotrophic larvae such as urchins, ophiuroids, and omnivorous asteroids. Thus, in this scenario, the early stages of succession would be characterised by heavily grazed barrens dominated by these taxa. From evidence in the present study and elsewhere (Chapter 3, Chapter 8 and references therein) such grazing can effectively prevent the establishment of sessile assemblages. For sessile taxa, therefore, the colonisation of recently exposed areas will be dependent on the availability of physical refugia or the attainment of a size refuge. The latter might be achieved through either rapid individual growth, or high densities of settlement resulting from short dispersal larvae. From the evidence available (Rauschert 1991, Osman & Whitlatch 2004, this study chapters 6 & 9), solitary ascidians exhibit a strategy of relatively wide dispersal followed by rapid growth. That so few ascidians survived on the settlement plates in this study also suggests that such strategies, based on the attainment of a size refuge through rapid growth of individuals, are high-risk. Pre-emption of substratum space through short dispersal and settlement close to conspecifics, as seen here in *Fenestrulina rugula*, might be a more conservative strategy by which an effective refuge in size from grazing is attained within a relatively short period, despite slow growth rates.

Directions for further research

Although this project has been largely successful in its main goals, there are several areas in which more intensive research is required to answer both specific and general ecological questions. These range from the local effects of urchin grazing, to the evolutionary consequences of developmental type. Common to all these questions, however, is the problem of interpreting results from relatively short-term, small-scale studies such as this in the context of environmental processes which operate over much

broader spatial, and longer temporal, scales. The most obvious directions for further work are in the following areas.

- The effects of biotic disturbances on assemblage development, and how these interact with gradients of physical disturbance by ice, clearly demand more detailed consideration than they have received to date. As a first investigation in the present study area, this might be most simply approached by urchin removal experiments. If grazing were the primary cause of post-settlement mortality, the abundance of sessile fauna would be predicted to increase in cleared treatments relative to controls. In combination with empirical data on the frequency of iceberg impacts at different depths this would indicate the extent to which sessile assemblages are controlled by grazing.

  At a broader spatial scale, initial indications from colonisation studies at Davis Station in east Antarctica are that urchin grazing there is of negligible importance (J. Stark, Australian Antarctic Division, pers. comm.). This suggests that studies of the large-scale demographics of *Sterechinus neumayeri* would be of interest, particularly in relation to historical patterns of glaciation and large scale hydrographic processes.

- The hypothesis that settlement timing in vagile taxa is dictated by the seasonal availability of food for the juvenile stages (Chapter 9) requires validation by accurate settlement-timing data for a wider range of species. This could be achieved in a number of ways but might be best approached by parallel field and laboratory studies. Laboratory rearing to metamorphosis of species with different developmental modes but similar adult diet would allow measurement of developmental periods and would enable feeding experiments to determine the dietary requirements of the juveniles. In combination with field recruitment studies aimed specifically at vagile rather than sessile fauna, such studies would provide accurate data on the larval period and timing of settlement. The specific, testable, prediction would be that all vagile predators and grazers will metamorphose and settle during the summer bloom, regardless of developmental mode.

- The trend for winter recruitment in sessile taxa here (Chapter 5) raises several questions. Ideally, the pattern of recruitment requires confirmation by year-

round recruitment data from other Antarctic locations. Indeed, the lack of directly comparable studies from other latitudes suggests a need for year-round studies of recruitment at monthly, or finer, resolution from both temperate and tropical environments. Such comparative studies are essential if general patterns are to be described and the processes underlying them are to be understood. An immediate next step from the present study, however, would be to compile species-level identifications for all winter-settling taxa. Comparison of settlement timings between endemic and non-endemic species, between species with different growth forms, and between early and late maturing species, might indicate whether winter settlement is a specific life history adaptation to the Antarctic nearshore environment, or a more general response to competitive pressures, evidence of which might be found at any latitude.

- Perhaps the most significant short-coming of studies such as this is the inability to identify larvae and early recruits reliably. Considering the importance of larval dispersal to the distributions of benthic organisms, the ability to identify larvae and relate them to source populations is a pressing need in the study of population dynamics at all scales. Molecular methods have great potential to overcome this (e.g. Olson et al. 1991, Hare et al. 2000, Gilg & Hilbish 2003) but their application to date has been limited and remains technically problematic, time-consuming, and expensive. Until we have affordable, high-throughput, identification methods for larvae it is unlikely that many more whole-assemblage, year-round, studies such as this will be undertaken. Indeed, the present study is only the fourth such investigation to have been undertaken anywhere in the world and three of these four studies have been conducted in polar seas (the latter two having been set up largely to test the theory generated by the first two). There is now a need for more detailed examinations of larval types, settling times, and particularly of realised dispersal distances in all latitudes if we are to identify general principles governing the establishment and maintenance of assemblages.

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Appendix A – recruit identifications

Appendix A – short term recruitment identifications

Table of identifications for recruits of sessile taxa on short-term recruitment plates (see photographs on attached CD: all images are filed by the taxon number in the left hand column, e.g. images of the first taxon in the table below are in the file "Taxon 30").

Taxon no.	ID code	Phylum	Class	Identity
30	Spo	Porifera	Demospongiae	Sponges
21	For	Rhizopoda		Foraminiferans
24	Fol	Ciliophora	Polyhymenophora	*Folliculina* sp.
25	FolEr	Ciliophora	Polyhymenophora	*Folliculina sp.* (erect type)
53	Rad1	Cnidaria	Alcyonaceae	*Primnoella* sp.
17	Hy	Cnidaria	Hydroida	Hydrozoans (stoloniferous)
18	HyEr	Cnidaria	Hydroida	Hydrozoans (erect)
48	[CD5_08.02#13]	Cnidaria		Indeterminate cnidarian
1	Serp	Annelida	Polychaeta	Serpulid polychaetes
2	Sp	Annelida	Polychaeta	Spirorbid polychaetes
19	Te	Annelida	Polychaeta	Terebellid polychaetes
22	Biv1	Mollusca	Bivalvia	*Adamussium colbecki*
44	Biv2	Mollusca	Bivalvia	*Phyllobrya* sp.
3	Cyc 1	Bryozoa	Stenolaemata	*Lichenopora/Discoporella* spp.
4	Cyc 2	Bryozoa	Stenolaemata	*Tubulipora/Idmidronea* spp.
5	Ai	Bryozoa	Gymnolaemata	*Aimulosia antarctica*
6	Hi	Bryozoa	Gymnolaemata	*Hippandanella inerma*
7	Ar	Bryozoa	Gymnolaemata	*Arachnopusia inchoata*
8	Bry OY	Bryozoa	Gymnolaemata	*Chaperiopsis protecta*
9	F	Bryozoa	Gymnolaemata	*Fenestrulina rugula*
10	MiN	Bryozoa	Gymnolaemata	*Micropora notialis*
11	MiB	Bryozoa	Gymnolaemata	*Micropora brevissima*
12	BryInd	Bryozoa	Gymnolaemata	Indeterminate cheilostome
13	Ca	Bryozoa	Gymnolaemata	*Celleporella antarctica*
14	Cd	Bryozoa	Gymnolaemata	*Celleporella dictyota*
15	Cb	Bryozoa	Gymnolaemata	*Celleporella bougainvillei*
16	Be	Bryozoa	Gymnolaemata	*Beania erecta*
32	CtB	Bryozoa	Gymnolaemata	*Camptoplites bicornis*
33	Os	Bryozoa	Gymnolaemata	*Osthimosia* sp.
34	Fi	Bryozoa	Gymnolaemata	*Figularia discors*
35	St	Bryozoa	Gymnolaemata	*Smittina* sp. 1
36	St2	Bryozoa	Gymnolaemata	*Smittina* sp. 2
37	El	Bryozoa	Gymnolaemata	*Ellisina antarctica*
38	LL	Bryozoa	Gymnolaemata	*Lageneschara lyrulata*
41	Ka	Bryozoa	Gymnolaemata	*Klugeflustra antarctica*

Appendix A (contd.)

Taxon no.	ID code	Phylum	Class	Identity
46	Noto	Bryozoa	Gymnolaemata	*Notoplites tenuis*
52	ErB2	Bryozoa	Gymnolaemata	Erect cheilostome, unidentified
54	ErB 4	Bryozoa	Gymnolaemata	Erect cheilostome, unidentified
45	Bry5?	Bryozoa		
49	Bry 6	Bryozoa		
28	Asc 1	Chordata	Ascidacea	Solitary ascidian, type 1 (yellow)
29	Asc 1*	Chordata	Ascidacea	Solitary ascidian, type 5 (star)
31	Asc 2	Chordata	Ascidacea	Solitary ascidian type 2 (pale)
39	Tu	Chordata	Ascidacea	Colonial tunicate
43	Asc 3	Chordata	Ascidacea	Solitary ascidian type 3 (orange)
50	??	Chordata	Ascidacea	Solitary ascidian type 4 *Ascidia* sp.
42	egg?	Indeterminate		Egg indet.
51	[BD1_11.09.02]	Indeterminate		
20	Li	Rhodophyta	Florideophyceae	Coralline algae

Appendix B – larvae identifications

Appendix B – larval identifications

(see photographs on attached CD: all images are labelled by the taxon number in the left hand column, e.g. images of the first taxon in the table below are labelled T022.jpg).

Taxon no.	Phylum	Class	Taxon	Larval stage	Adult mode	Authority
22	Porifera	Demospongiae	Haplosclerida	parenchymella	sessile	(Maldonado & Bergquist 2002)
32	Porifera	Demospongiae	Poecilosclerida	parenchymella	sessile	(Maldonado & Bergquist 2002)
51	Porifera	Demospongiae	Dictyoceratid	parenchymella	sessile	(Maldonado & Bergquist 2002)
136	Porifera	Demospongiae	Poecilosclerida	parenchymella	sessile	(Maldonado & Bergquist 2002)
7	Cnidaria	Hydrozoa		planula	sessile	(Hyman 1940, Martin & Koss 2002)
37	Cnidaria	Hydrozoa		actinula	sessile	
38	Cnidaria	Hydrozoa		medusa?	vagile	
63	Cnidaria			actinula	sessile	
113	Cnidaria	Anthozoa		planula	sessile	(Martin & Koss 2002)
116	Cnidaria	Hydrozoa		planula	sessile	
133	Cnidaria	Hydrozoa		planula	sessile	(Martin & Koss 2002)
139	Cnidaria	Anthozoa		planula	sessile	(Martin & Koss 2002)
125	Cnidaria	Anthozoa		planula	sessile	(Martin & Koss 2002)
85	Ctenophora	Lobata		cydippid	planktonic	(Martindale 2002)
106	Ctenophora	Lobata		cydippid	planktonic	(Martindale 2002)
67	Platyhelminthes			muller	vagile	(Smith et al. 2002)
2	Nemertea	Anopla	Heteronemertea	pilidium	vagile	(Peck 1993)
4	Nemertea	Anopla	Heteronemertea	juvenile	vagile	personal observation
6	Nemertea	Anopla	Heteronemertea	pilidium	vagile	
39	Nemertea	Anopla		juvenile	vagile	personal observation

Taxon no.	Phylum	Class	Taxon	Larval stage	Adult mode	Authority
56	Nemertea	Anopla		juvenile	vagile	Personal observation
79	Nemertea	Anopla		juvenile	vagile	
11	Annellida	Polychaeta	Polynoid	late nectochaete/juvenile	vagile	
12	Annellida	Polychaeta		juvenile	vagile	
13	Annellida	Polychaeta	Spionid	nectochaete/juvenile	vagile	(Scheltema et al. 1997, Pernet et al. 2002)
14	Annellida	Polychaeta	Syllid	nectochaete/juvenile	vagile	
16	Annellida	Polychaeta	Sabellariid	nectochaete	vagile	(Pernet et al. 2002)
17	Annellida	Polychaeta		trochophore	vagile	
19	Annellida	Polychaeta		trochophore	vagile	
20	Annellida	Polychaeta	Syllid	trochophore/nectochaete	vagile	
20a	Annellida	Polychaeta	Syllid	trochophore	vagile	
21	Annellida	Polychaeta		trochophore/nectochaete	vagile	
21a	Annellida	Polychaeta		trochophore	vagile	
24	Annellida	Polychaeta	Terebellid	nectochaete/juvenile	vagile	(Pernet et al. 2002)
25	Annellida	Polychaeta	Spirorbid	trochophore	vagile	personal observation
26	Annellida	Polychaeta	Spirorbid	metatrochophore	sessile	personal observation
49	Annellida	Polychaeta	Spirorbid	nectochaete	sessile	personal observation
50	Annellida	Polychaeta		nectochaete	vagile	
59	Annellida	Polychaeta		nectochaete	vagile	
62	Annellida	Polychaeta		trochophore/nectochaete	vagile	
66	Annellida	Polychaeta		nectochaete	vagile	
68	Annellida	Polychaeta		juvenile	vagile	

Taxon no.	Phylum	Class	Taxon	Larval stage	Adult mode	Authority
69	Annellida	Polychaeta		juvenile	vagile	
71	Annellida	Polychaeta		nectochaete/juvenile	vagile	
82	Annellida	Polychaeta		juvenile	vagile	
80	Annellida	Polychaeta	*Flaberigella mundata*	juvenile	vagile	
89	Annellida	Polychaeta		trochophore		
92	Annellida	Polychaeta		juvenile	vagile	
110	Annellida	Polychaeta	*Tomopteris* sp.	juvenile	planktonic	(Hayward & Ryland 1995)
115	Annellida	Polychaeta		nectochaete	vagile	
117	Annellida	Polychaeta		nectochaete	vagile	
128	Annellida	Polychaeta			vagile	
130	Annellida	Polychaeta	Polynoid	trochophore/early nectochaete	vagile	
131	Annellida	Polychaeta	Polynoid	trochophore	vagile	
134	Annellida	Polychaeta		trochophore/early nectochaete	vagile	
141	Annellida	Polychaeta		nectochaete/juvenile	vagile	
10	Mollusca	Gastropoda	*Capulus* sp.	echinospira	vagile	(Hain & Arnaud 1992)
28	Mollusca	Gastropoda	Opisthobranchia	veliger	vagile	Stanwell-Smith et al (1997), Todd pers comm
28a	Mollusca	Gastropoda		juvenile	vagile	
36	Mollusca	Gastropoda		veliger	vagile	
40	Mollusca	Pteropoda	*Limacina* sp.	veliger	planktonic	
44	Mollusca	Pteropoda	*Clione* sp.	polytrochous larva	planktonic	(Buckland-Nicks et al. 2002)
53	Mollusca	Bivalvia	*Adamussium colbecki*	veliger	vagile	(Berkman et al. 1991, and K. Linse pers com)
70	Mollusca			trochophore	vagile	

Taxon no.	Phylum	Class	Taxon	Larval stage	Adult mode	Authority
83	Mollusca	Bivalvia	Philobryidae	veliger	sessile	(Hain & Arnaud 1992)
88	Mollusca	Polyplacophora	chiton	pseudotrochophora	vagile	(Hain & Arnaud 1992)
103	Mollusca			trochophore	vagile	Stanwell-Smith et al (1997)
107	Mollusca			veliger	vagile	
118	Mollusca	Gastropoda		veliger	vagile	
124	Mollusca	Gastropoda	*Nacella concinna?*	veliger	vagile	(Buckland-Nicks et al. 2002)
18	Echiura/Sipunculida			trochophore/pelagosphera	vagile	
18a	Echiura/Sipunculida			trochophore/pelagosphera	vagile	
57	Echiura/Sipunculida			trochophore/pelagosphera	vagile	
27	Bryozoa	Gymnolaemata	Bryozoan	coronate	sessile	personal observation
33	Bryozoa	Gymnolaemata	*Alcyonidium* sp.	cyphonautes	sessile	(Shreeve & Hayward 1995)
97	Brachiopoda	Articulata	*Liothyrella uva*	3-lobed	sessile	(Peck & Robinson 1994)
23	Echinodermata	Asteroidea	*Odontaster*	gastrula/bipinnaria	vagile	Stanwell-Smith et al (1997)
23a	Echinodermata	Asteroidea	*Odontaster*	early gastrula	vagile	Stanwell-Smith et al (1997)
31	Echinodermata	Asteroidea	*Odontaster*	gastrula	vagile	Stanwell-Smith et al (1997)
34	Echinodermata	Asteroidea		brachiolaria	vagile	
74	Echinodermata	Asteroidea		bipinnaria	vagile	
35	Echinodermata	Echinoidea	*Sterechinus neumayeri*	echinopluteus	vagile	
41	Echinodermata	Echinoidea	*Sterechinus neumayeri*	juvenile	vagile	
108	Echinodermata	Echinoidea	*Sterechinus neumayeri*	gastrula	vagile	
47	Echinodermata	Holothuroidea/ Crinoidea		doliolaria	vagile	(Sewell & McEuen 2002)

Taxon no.	Phylum	Class	Taxon	Larval stage	Adult mode	Authority
60	Echinodermata	Holothuroidea		pentacula	vagile	
72	Echinodermata	Holothuroidea/ Crinoidea		doliolaria	vagile	
105	Echinodermata	Holothuroidea		pentacula	vagile	
100	Echinodermata	Asteroidea		bipinnaria	vagile	
101	Echinodermata	Asteroidea		bipinnaria	vagile	
102	Echinodermata	Asteroidea		bipinnaria	vagile	
120	Echinodermata	Holothuroidea/ Crinoidea		doliolaria	vagile	
127	Echinodermata	Holothuroidea		pentacula	vagile	
114	Echinodermata	Ophiuroidea		ophiopluteus	vagile	
123	Echinodermata	Ophiuroidea		early ophiopluteus	vagile	
95	Echinodermata	indet		gastrula	vagile	
42	Chordata	Ascidiacia		tadpole	sessile	
43a	Chordata	Ascidiacia		egg	sessile	
86	Chordata	Ascidiacia		tadpole	sessile	
87	Chordata	Ascidiacia		egg	sessile	
104	Chordata	Ascidiacia		egg	sessile	
112	Chordata	Ascidiacia		tadpole	sessile	
30	indet			planula		
45	indet					
46	indet			trochophore		
48	indet			planula		

Taxon no.	Phylum	Class	Taxon	Larval stage	Adult mode	Authority
55	indet			planula		
61	indet			planula		
65	indet			trochophore		
73	indet					
75	indet			planula		
76	indet					
77	indet			planula		
81	indet			egg		
84	indet					
93	indet					
94	indet			planula		
96	indet			planula		
98	indet					
99	indet					
109	indet			planula		
119	indet					
122	indet					
129	indet					
132	indet					
3	indet			gastrula		
126	indet					
135	indet			trochophore		

Taxon no.	Phylum	Class	Taxon	Larval stage	Adult mode	Authority
137	indet					
138	indet					
140	indet					

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Data and image library CD

(Affixed to back cover)